Volume 49, Number 1

February 1975

Northwest Science

1 Geomorphic History of the Lower Blue River-Lookout Creek Area, Western Cascades, Oregon
Frederick J. Swanson and Michael E. James

12 Body Measurements of Western Jumping Mice from Northwestern Wyoming
Tim W. Clark

14 Ecological Notes on Deer Mice in Grand Teton National Park, Wyoming
Tim W. Clark

17 Phenological Patterns of Two Alpine Tundra Plant Populations on Niwot Ridge, Colorado
M. Fareed and M. M. Caldwell

24 Ecology of Artemisia tridentata subsp. tridentata in the State of Washington
R. Daubenmire

36 Plant Succession on Abandoned Fields, and Fire Influences, in a Steppe Area in Southeastern Washington
R. Daubenmire

Official Publication of the Northwest Scientific Association

US ISSN 0029—344X

Northwest Science

Volume 49, Number 1, February 1975

The Northwest Scientific Association is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association which includes a subscription to Northwest Science is $5.00 per year. Except $2.00 per year for students, institutional membership: less than 3000 students, $15.00; 3000 students or more, $30.00. Supporting memberships: minimum of $10.00 per year for individuals and $50.00 per year for organizations, institutions, or agencies.

Payment should be made to the Treasurer.

Editor
Bruce V. Ettling
Department of Materials Science
Washington State University
Pullman, Washington 99163

Officers of the Association

President
John S. Shrader
Central Washington State College
Ellensburg, Washington (1976)*

Vice-President
Ernest Gilmour
Eastern Washington State College
Cheney, Washington (1975)

Secretary
Milton M. Mosher
Washington State University
Pullman, Washington (1975)

Treasurer
Richard J. Naskali
Department of Biological Sciences
University of Idaho
Moscow, Idaho (1975)

Honorary Trustees
Royce Cox
Philatelli Corp.
Lewiston, Idaho (1975)

Edward Harrington
Central Washington State College
Ellensburg, Washington (1975)

S. Roger Ray
Washington State University
Pullman, Washington (1975)

Trustees
W. Louis Barratt
Western Washington State College
Bellingham, Wash. (1975)

George Blake
University of Montana
Missoula, Mont. (1975)

Harry H. Caldwell
University of Idaho
Moscow, Idaho (1975)

William J. Dilliard
Western Washington State College
Bellingham, Wash. (1977)

C. Theodore Dyrness
U.S. Forest Service
Fairbanks, Alaska (1977)

Jack Fletcher
University of British Columbia
Vancouver, B.C. (1976)

Charles F. Hecther
Bureau of Sport Fisheries
Olympia, Wash. (1977)

Kenneth Holmes
Oregon College of Education
Monmouth, Oregon (1976)

Glen Klock
U.S. Forest Service
Wenatchee, Wash. (1976)

L. M. Laykulich
University of British Columbia
Vancouver, B.C. (1977)

Edwin A. Olson
Whitworth College
Spokane, Wash. (1975)

Patricia Packard
College of Idaho
Caldwell, Idaho (1976)

Dale Strasling
Eastern Washington State College
Cheney, Wash. (1976)

David R. Stranck
Washington State University
Pullman, Wash. (1977)

Oscar Szikla
University of British Columbia
Vancouver, B.C. (1975)

*Term of office expires in the year given in parentheses.

PUBLISHED QUARTERLY BY WASHINGTON STATE UNIVERSITY PRESS
WITH COLLABORATION OF NORTHWEST SCIENTIFIC ASSOCIATION

Frederick J. Swanson
and
Michael E. James
Geology Department
University of Oregon
Eugene, Oregon

Geomorphic History of the Lower Blue River-Lookout Creek Area, Western Cascades, Oregon

Abstract

The landscape of lower Blue River and Lookout Creek has been formed by glacial, alluvial, and mass wasting processes. More than 40,000 radiocarbon years b.p. a glacier moved up into the Blue River drainage from the main McKenzie River valley. In the process, the mouth of Blue River valley was choked with ice and glacial sediment, forcing the river to establish a new, westerly course. The ice dam also formed a lake in which fine-grained sediments were deposited.

After retreat of the pre-40,000 years b.p. glacier, Blue River began to erode the valley fill. However, during the latest Wisconsin glaciation and deglaciation the rivers again aggraded. Subsequent downcutting resulted in the development of a prominent terrace. Terrace sediments are topped by Mazama ash, indicating that this surface was abandoned as a floodplain by about 7000 radiocarbon years b.p. The modern floodplain forms a lower surface cut into glacial sediments.

Alluvial fans from tributary watersheds have been constructed onto the landforms of the valley floor. The size, degree of dissection, and internal make-up of the fans is directly related to terrace-floodplain width and watershed characteristics, especially area, relief, and bedrock geology. Fans at the mouths of larger watersheds (about 40 to 200 ha) are deeply dissected by the tributary stream and had stopped growing by Mazama-ash time. Many smaller watersheds, on the other hand, continue to construct small fans in which Mazama ash may be buried up to 4 m deep.

Introduction

The Western Cascade Range of Oregon is an area of heavily forested, steep, and somewhat unstable terrain. Studies by Anderson (1954), Dyrness (1967), Fredriksen (1970), and others have shown that forest management practices on these timber lands have had an important impact on rates of soil erosion and therefore on forest productivity. For this reason the U.S. Forest Service and the Coniferous Forest Biome of the International Biological Program have been conducting studies of erosion in the H. J. Andrews Experimental Forest 80 km east of Eugene.

This paper describes a part of the work focusing on the alluvial and glacial history in the vicinity of five research watersheds. Our purpose has been to understand better the geomorphic setting of the watersheds and to delineate and date geomorphic surfaces for soil studies now in progress. A long-range aim of the project is to develop means of estimating geologic rates of erosion and to compare them with contemporary erosion rates in areas influenced by timber management activities. The fact that no previous detailed geomorphic work had been done in the region necessitated this background study.

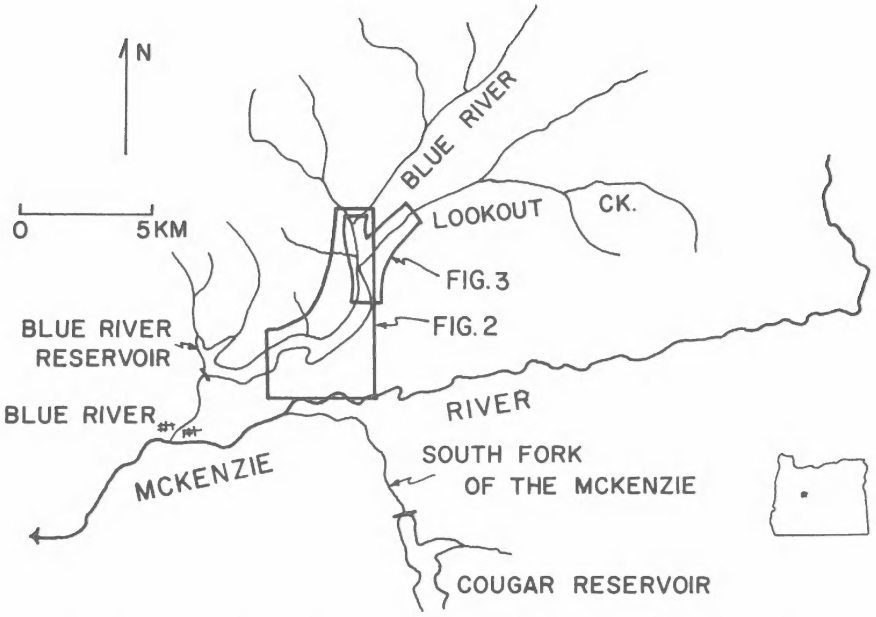


Figure 1. Index map of the lower Blue River area about 80 km east of Eugene, Oregon.

General Geologic and Geomorphic Settings

The earliest known history of the present Blue River area (Fig. 1) began in Oligocene and Miocene time with the eruption of volcanic rocks of the Little Butte and Sardine Formations (Peck *et al.*, 1964). In post-Sardine time there was a hiatus of several million years before eruption of Pliocene-age pyroclastic rocks and lava flows, which erased the earlier topography (E. M. Taylor, Oregon State University, and A. R. McBirney, University of Oregon, personal communications).

Thus the geomorphic history of the modern Blue River drainage began about four million years ago. Since that time the landscape has been carved out by the combined forces of tectonic uplift, stream erosion, mass wasting, and glaciation. Although the rapid erosional processes have removed most evidence of the geomorphic history of the area before late Quaternary time, more recent glacial and alluvial processes have clearly left their marks in the sedimentary record and on the drainage pattern of lower Blue River.

Glacial and Physiographic History

Both sedimentary and physiographic evidence indicates that during one or more periods of glaciation, glaciers from the McKenzie River valley moved several kilometers up into the Blue River drainage (Fig. 1). The primary path of ice movement was upstream through the low divide (410 m elevation) now occupied by the saddle dam of the Blue River reservoir (in the vicinity of section A-A′ in Fig. 2). There are also indications that ice from the McKenzie valley spilled into Blue River through a 640-m-elevation saddle in Lookout Ridge east-southeast of location 1 in Figure 2.

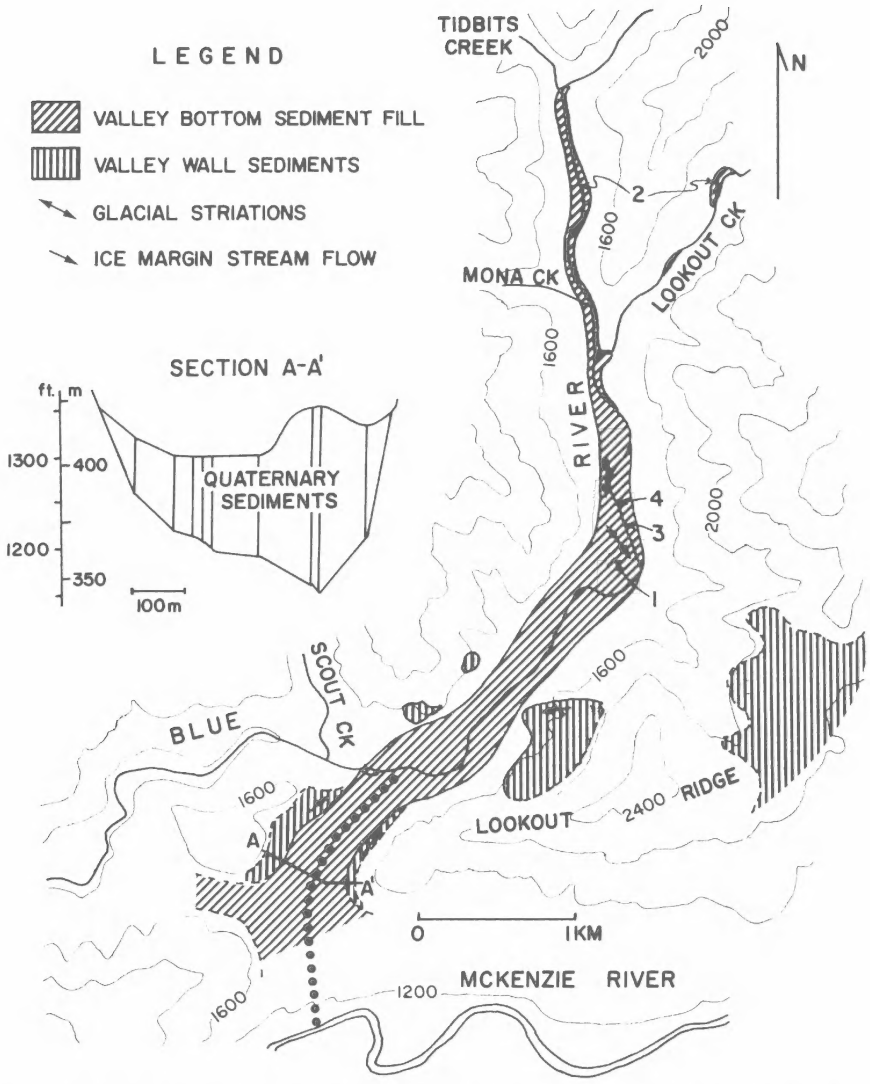


Figure 2. Map showing distribution of fluvial and lacustrine sediments related to glaciation of lower Blue River. Location 1 notes the occurrence of N25W-trending glacial striations. Location 2 marks sedimentary sections in the upper end of the lake, while at location 3 there are good exposures of sediments deposited in the lower portion of the lake. Wood collected from glacio-lacustrine sediments at location 4 was dated at >40,000 years b.p. Dotted line shows former course of Blue River. Contours (interval = 400 ft) from U.S. Geological Survey Blue River and McKenzie Bridge 15-ft quadrangles. Cross-section was drawn from U.S. Army Corps of Engineers' data.

Excavations by the U.S. Army Corps of Engineers at location 1 have exposed a glacially striated bedrock surface with patches of till plastered on it. The striae trend N25W, directly in line with the Lookout Ridge saddle, rather than parallel to the south

to south-southwest orientation of the valley axis. Further evidence that ice may have flowed over the ridge has been observed during field reconnaissance in the main McKenzie valley, where patches of weathered till and kame terrace deposits indicate that ice probably reached at least as high as the 2400-ft contour (732 m).

Till is observed in scattered exposures along Blue River for a distance of 1.3 km upstream from location 1 (Fig. 2). The till occurs in several beds up to 2 m thick which are interbedded with fluvial sand and gravel and quiet water silt and clay deposits. In several instances the sediments appear to have been overridden by glacial advance in the upstream direction. The stratigraphy of this section records at least three upstream advances and downstream retreats. Absence of any old weathering surfaces suggests that these ice-front fluctuations occurred over a relatively short period of time, probably during a single glacial epoch.

While glaciers were present in the lower Blue River valley, stream drainages developed along the margins of the ice and resulted in the accumulation of river gravel in kame terraces deposited against the valley walls. Remnants of these deposits are located as "valley wall sediments" in Figure 2, and arrows indicate direction of stream flow based on stone imbrication and cross-bed orientation.

Ice in the mouth of Blue River also dammed up a lake which reached an elevation of at least 425 m (1400 ft) and extended 1.5 km up into the Lookout Creek drainage and along Blue River to a point just above the mouth of Tidbits Creek. Sections up to 7 m thick of fine-grained, quiet-water sediments are exposed in the upper and lower ends of the lake basin (locations 2 and 3, respectively, in Fig. 2).

The shape of Blue River valley before it was partially filled with sediment may be roughly determined from subsurface information gathered by the Corps of Engineers during construction of the reservoir. They drilled a series of holes across the saddle (shown as profile A-A′ in Fig. 2), which penetrated up to 78 m of semiconsolidated sediments before reaching bedrock. Other exploratory drilling and back-hoe trenching by the Corps have determined that this sedimentary fill forms a wedge which thins upstream from the saddle dam area until it pinches out near the mouth of Mona Creek (Fig. 2).

These observations indicate that Blue River formerly flowed through a canyon where the saddle dam is now located (Fig. 2) and joined with the McKenzie about 5 km upstream from their present confluence (Fig. 1). A shift of the drainage pattern occurred when glaciers filled the main McKenzie valley and ice pushed up into the Blue River drainage. Blockage of the channel diverted the course of Blue River over a low divide into the next drainage to the west. After retreat of the ice sufficient glacial debris and fluvial and lacustrine sediments filled the old channel to prevent re-establishment of the earlier stream pattern.

The physiography of Blue River valley reflects this glacial history. The river flows over bedrock at the head of the reservoir and near the mouth of Scout Creek, where it makes a westward turn at the beginning of the ice-barrier-diverted section of the river. Between these points the channel and older alluvial landforms of Blue River are cut into the soft Quaternary sediment which is in part preserved because the river is graded to the lower bedrock bench. Consequently the valley is broad and flat along this reach of the river and narrows into the bedrock channels both up and downstream.

The ice which filled the McKenzie valley and changed the course of lower Blue River was derived principally from the High Cascade plateau and the South Fork drainage. The distribution of cirques and glacial deposits in upper parts of the Blue River and Lookout Creek watersheds suggests that during the period for which there is a sedimentary record, these relatively low elevation catchments did not supply glaciers of sufficient size to extend into the map area of Figure 2. However, one cannot rule out the possibility that earlier glaciations may have inundated all of these valleys and that the evidence was subsequently eroded from the steep valley walls.

With the use of radiocarbon dating of wood fragments it is possible to place some limit on the age of glaciation of lower Blue River. One sample of Pacific yew (*Taxus brevifolia*) collected from fluvial sediments interbedded with till (location 4, Fig. 2) was dated at more than 40,000 years b.p. A second sample, western hemlock (*Tsuga heterophylla*) or incense cedar (*Librocedrus decurrens*), was collected from a probable debris torrent deposit immediately underlying glaciofluvial sediments exposed in the bank of Lookout Creek 1.2 km from its mouth. The age of the wood is greater than 35,500 radiocarbon years b.p. These dates indicate that the movement of glaciers into lower Blue River from the main McKenzie River valley occurred before 40,000 radiocarbon years ago.

Alluvial History of the Blue River-Lookout Creek Area

After the pre-40,000 years b.p. glaciation and the resulting aggradation of the lower Blue River valley, the river began to exhume its old channel. We have no record of the geomorphic history of the valley for an unknown period during the early history of this excavation. However, since the time of the latest Wisconsin glacial maximum, various alluvial landforms have preserved a clear history of alluviation, subsequent downcutting, and the construction of alluvial terraces and fans.

The task of unraveling this history has been greatly assisted by the occurrence of a volcanic ash layer on top of, or buried within, some landforms. The ash serves as an excellent time horizon because it can be correlated by petrographic methods with known Mazama airfall tephra, which were erupted approximately 7000 radiocarbon years ago (Kittleman, 1973). That eruption blanketed the Blue River region with about 1 cm of pumiceous ash.

Fluvial Terrace and Floodplain History

In the mapped area a distinct terrace surface (the "fluvial terrace" in Fig. 3) stands 6 to 10 m above the present channel. The base of the terrace is cut onto the glacial deposits and Tertiary bedrock. Terrace deposits are typically composed of up to 5 m of well-rounded, imbricated cobbles and boulders with minor fine gravel and sand interbeds which generally grade upward to a meter or so of unstratified silt to coarse sand overbank material. In some exposures a layer of Mazama ash occurs within or immediately overlies overbank sediments, and these units may be buried beneath subangular to subrounded, poorly sorted gravels from tributary watersheds. Therefore we can infer that mainstream deposition on the terrace surface was completed about 7000 radiocarbon years b.p. and that by that time Blue River and Lookout Creek were incising deeper channels.

A minimum age of 7000 years for the fluvial terrace suggests that it may be

correlative with the Winkle geomorphic unit mapped by Balster and Parsons (1968) in the Willamette Valley. They report Mazama ash in the upper meter of alluvium under the Winkle surface and obtained a radiocarbon age of 5250 ± 270 years for an Indian hearth under a soil on the surface. Although correlations of geomorphic surfaces may be tenuous, it does seem reasonable that the Blue River terrace and the Winkle surface in the Willamette Valley were developed as floodplains in response to a single, but not necessarily synchronous, regional adjustment of fluvial regimens to climate and vegetation changes after retreat of the latest Wisconsin glaciers. Subsequent downcutting by local streams has caused the Winkle-age surface to be abandoned as a floodplain.

The modern vegetated floodplains of Blue River and Lookout Creek form a geomorphic surface 1 to 2 m above present low water level. In most cases this surface has been cut onto glacial sediments. In fact, the presence of the easily eroded, older Quaternary sediments appears to control the geographic distribution of the surface. Several Douglas-fir trees (*Pseudotsuga menziesii*) more than 400 years old have recently been cut from one segment of the floodplain, suggesting a minimum age for the floodplain of 400 to 500 years and indicating that the modern channel has been in its present position for at least that length of time. The floodplain characteristics and age are similar to those of the Ingram geomorphic unit of Balster and Parsons (1968), which they dated at 550 to 3200 years b.p.

The presently active channels of Blue River and Lookout Creek are mapped in Figure 3 as "modern channels." The two streams flow on bedrock and modern alluvium above their confluence, and below that point the channel is cut into the glacial sediments. The modern channels correspond to the Horseshoe surface of Balster and Parsons (1968).

Alluvial Fan History

In the Blue River-Lookout Creek area alluvial fans have been constructed onto the floodplain and terrace surfaces from the mouths of tributary watersheds. The general morphology of two types of fans is sketched in Figure 4. Upper surfaces of the fans dip radially 5° to 10° from their apex.

The fans have been constructed by two types of stream-channel processes. Sediment is deposited from bedload and from suspended load during high discharge events of recurrence intervals ranging upward from several per year. Fans may also accumulate sediment by deposition from episodic debris torrents which may flush large masses of rocks, mud, logs, and sticks from channels in a matter of seconds or minutes (Fredriksen, 1963). Debris torrents may be triggered by mass movements into the channel or the breakup of pre-existing debris dams in the channel during exceptionally high peak discharges. The average recurrence interval of such events is not known, but, judging from Fredriksen's (1965) observations, 50 to 200 years seems to be a reasonable estimate.

The characteristics of individual fans, in terms of their size, morphology, internal stratigraphy, and extent of erosion by the tributary and mainstreams, are functions of floodplain width and watershed variables such as area, channel length, relief, and slope stability. Within the mapped area it is possible to delineate two types of fans on the basis of probable history and present stage of development. However, there is

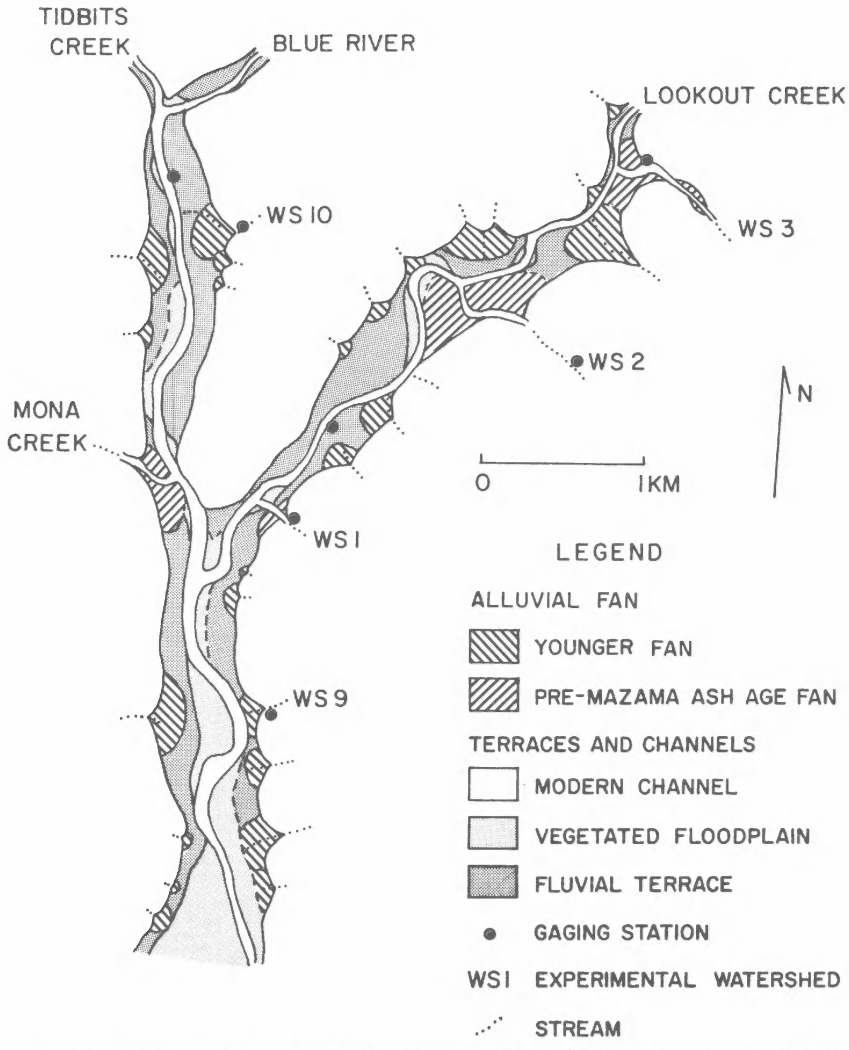


Figure 3. Map of post-glacial geomorphic surfaces near the confluence of Blue River and Lookout Creek.

a continuum of fan characteristics and, therefore, distinguishing fan types is somewhat subjective.

Alluvial fans labeled as "pre-Mazama ash age" in Figure 3 were constructed at the mouths of larger tributary watersheds (approximately 40 to 200 ha) primarily by the accumulation of debris torrent material. This is most clearly seen in the case of watershed 3, where a roadcut exposes a 15-m, vertical section of the fan interior composed of a series of beds up to several meters in thickness. Individual depositional units are made up of subangular, unsorted mineral material, ranging from clay size

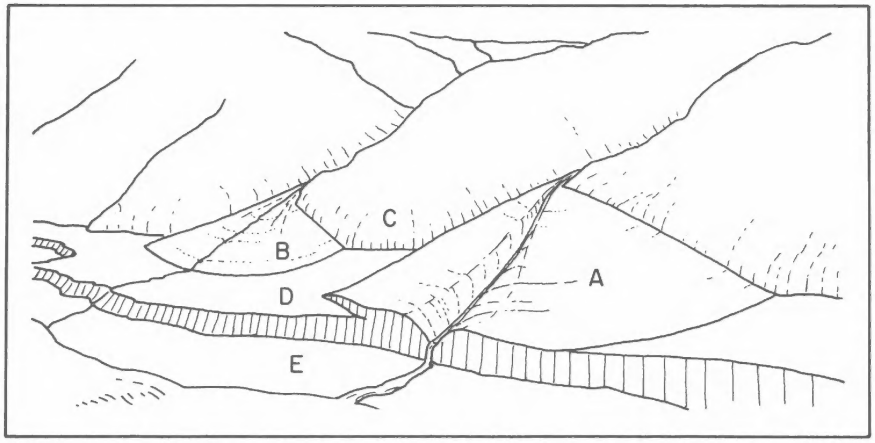


Figure 4. Sketch of two types of alluvial fans. A = dissected pre-Mazama ash age fan; B = young, active fan; C = hillslope; D = fluvial terrace; E = floodplain. Sketch by Ray Wells.

to blocks 1.7 m long, but with a notable absence of woody matter. Scattered patches of Mazama ash are found on or near the fan surface.

This internal stratigraphy indicates that the fans were formed by periodic debris torrents before about 7000 years ago. The paucity of wood in the old deposits contrasts strikingly with modern, log-filled, debris torrent material (Fredriksen, 1963, 1965). The difference may in part be related to an increase in the amount of organic debris in stream channels because of logging activities or may be due to a natural bias in the sample, such as loss of organic material by decomposition. However, this difference in wood deposits may also reflect the presence of much sparser vegetation during the period of deposition—possibly scattered groves of lodgepole pine (*Pinus contorta*) with only minor amounts of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) (Heusser, 1960).

Morphology of pre-Mazama ash age fans was greatly modified during and after fan construction by mainstream overbank flow on the terrace surface and by downcutting of both mainstream and tributary channels (Fig. 4). In larger watersheds drained by perennial streams, channels were cut into the fans between debris torrent events. As the fan surface aggraded and downcutting by the tributary stream continued, the channel eventually became so deeply incised that fan construction ceased. This had occurred by the time of the Mazama ash fall, and subsequent debris torrents passed directly through the fan area and into the mainstream channel. The process of fan dissection was accelerated by downcutting of the mainstream channel which served to lower local base level.

Fans built at the mouths of smaller watersheds (less than about 40 ha) are generally composed of better sorted and finer sediments than the pre-Mazama ash age fans. An additional important distinction is that where the floodplain is broad enough to contain much of the fan, the surface of a fan from a small watershed is still aggrading or is gullied to a depth of no more than 1.5 m by the tributary stream.

In the small watershed fans, beds of stream-transported Mazama ash up to 25 cm

in thickness are buried as much as 4 m below the fan surface. Such a stratigraphy indicates that these fans continued to accumulate sediment long after the pre-Mazama ash fans had stopped growing. For this reason small watershed fans are designated "younger" in Figure 3. Some of the alluvial fans containing ash layers offer a rather complete record of the erosional debris removed from a watershed for a time period extending back more than 7000 years. Future study of these fans will yield information about long-term processes and rates of erosion.

The finer grained, better sorted characteristics of sediment composing small watershed fans indicate that the fans were constructed by deposition of material transported as bedload or suspended load. On some of the fans, debris torrents have deposited coarse, unsorted material which has been reworked on the fan surface by more frequent, lower-magnitude alluvial events. In this manner sediment characteristics may offer a somewhat biased record of the processes transporting material to the fans.

The apparent contrast in the primary constructional processes for younger fans (annual scale events) and older fans (infrequent catastrophic debris torrents) is mainly a consequence of differences in watershed characteristics; but this contrast may also be related to a change in the relative rates of geomorphic processes about 7000 radiocarbon years ago, due to changing vegetation and climate in post-glacial times. A further complicating factor is that the older fans probably do not preserve a record of much of the alluvium which was carried in sediment transport events of low to moderate magnitude. Most of this material appears to have been transported directly through the stream channel cutting across the fan.

However, there are a number of reasons for believing that larger watersheds are more susceptible to massive debris torrent events. Geological considerations appear to be the major factors. Dyrness (1967), Fredriksen (1970), and others have pointed out that mass movements often initiate debris torrent events in channels. Dyrness (1967) has further shown that within the Andrews Experimental Forest there is a marked tendency for mass soil movements to occur at elevations between 610 and 800 m. This altitudinal band is the zone of transition from predominantly deeply weathered and altered volcanoclastic rocks below to relatively fresh lava flows at higher elevations. The underlying volcanoclastic rocks are much more susceptible to erosion by mass movements and stream cutting. The capping effect of the more resistant flow rocks prevents the establishment of a stable slope profile. As a result the clastic rocks are left in a highly unstable, over-steepened condition, and the contact zone is consequently the site of numerous shallow and deep-seated earth failures and the initiation point for debris torrents. In this way the geological setting contributes substantially to landscape instability and the initiation of debris torrents in the upper parts of the large watersheds. Headwaters of smaller watersheds in the study area do not extend high enough to reach critical exposures of the ridge capping flows.

Several other aspects of watershed size also appear to influence sediment discharge characteristics. One factor is that longer channels offer a greater chance for the development of debris dams, which may fail and trigger debris torrents at times of high peak flows during storms. Streams in larger watersheds are also subjected to extreme peak discharges, great enough to break up debris dams and flush the channels. In addition there may be meteorological factors such as greater chance of snowmelt runoff at higher elevations, which would tend to increase the probability of periodic scouring

of channels in larger watersheds. However, at this time we do not have sufficient data for detailed analysis of these hypothetical relationships.

Summary

The interplay of glacial, alluvial, and mass movement processes has determined the geomorphic history of the lower Blue River and Lookout Creek valleys. More than 40,000 radiocarbon years b.p. a glacier from the McKenzie River valley moved up into the Blue River drainage, depositing as much as 65 m of sedimentary fill in the former mouth of the river and forcing Blue River to establish a new, westerly course. The ice dammed Blue River, backing a lake up the main stream and into its tributary, Lookout Creek, to approximately 1.5 km above the confluence of the two. Below the mouth of Lookout Creek the river is cut into glacial, lacustrine, fluvial, and till deposits.

After retreat of the glacier the river began to cut down through the valley fill. However, there was a fresh influx of sediment during, and just after, the latest Wisconsin glaciation of upper Lookout Creek and Blue River which resulted in channel aggradation. The subsequent period of downcutting led to the deveolpment of a prominent terrace. Fluvial sediments making up the terrace deposits are topped by Mazama ash, indicating that this surface was abandoned as a floodplain about 7000 radiocarbon years b.p. The modern floodplain, a lower surface, was cut into glacial sediments and appears to have maintained its present configuration for at least the past 400 to 500 years.

Alluvial fans from the tributary watersheds have been constructed on the floodplain and terrace surfaces. The size, degree of dissection, and internal make-up of the fans are directly tied to terrace-floodplain width and watershed characteristics, especially area, relief, and bedrock geology. Fans at the mouths of larger watersheds (approximately 40 to 200 ha) were constructed primarily from deposition by debris torrents before the Mazama ash fall occurred. Since that time these fans have been deeply incised by the tributary and main streams. In smaller watersheds more frequent, less catastrophic alluvial events have been the dominant agents of fan construction. Surfaces of many of these fans are still aggrading and the Mazama ash is buried up to 4 m within them.

Acknowledgements

This study was supported by National Science Foundation Grant No. GB-20963 to the Coniferous Forest Biome, U.S. Analysis of Ecosystems, International Biological Program. We thank C. T. Dyrness, R. L. Fredriksen, D. N. Swanston, R. B. Parsons, R. B. Brown, and L. R. Kittleman for helpful discussions during various phases of the work. The first five people listed above also reviewed a draft of the manuscript. Dr. Parsons, Soil Conservation Service, obtained the radiocarbon dates from Teledyne Isotopes, Westwood, N.J. Identification of wood samples was made by A. Doerksen, Forest Research Lab., Oregon State University. George Adams kindly gave us access to Army Corps of Engineers' data. This is contribution No. 108 from the Coniferous Forest Biome.

Literature Cited

Anderson, H. W. 1954. Suspended sediment discharge as related to stream flow, topography, soil, and land use. Trans. Amer. Geophys. Union. 35: 268-281.

Balster, C. A., and R. B. Parsons. 1968. Geomorphology and Soils, Willamette Valley, Oregon. Agricultural Exper. Station, Oregon State Univ., Corvallis, Spec. Rep. 265. 31 p.

Dyrness, C. T. 1967. Mass Soil Movements in the H. J. Andrews Experimental Forest. USDA For. Serv. Res. Paper PNW-42. 12 p.

Fredriksen, R. L. 1963. A Case History of a Mud and Rock Slide on an Experimental Watershed. USDA For. Serv. Res. Note PNW-1. 4 p.

———. 1965. Christmas Storm Damage on the H. J. Andrews Experimental Forest. USDA For. Serv. Res. Note PNW-29. 11 p.

———. 1970. Erosion and Sedimentation Following Road Construction and Timber Harvest on Unstable Soils in Three Small Western Oregon Watersheds. USDA For. Serv. Res. Paper PNW-104. 15 p.

Heusser, C. J. 1960. Late-Pleistocene Environments of North Pacific North America. Amer. Geog. Soc., Spec. Pub. No. 35. 308 p.

Kittleman, L. R. 1973. Mineralogy, correlation, and grain-size distribution of Mazama tephra and other post-glacial pyroclastic layers, Pacific Northwest. Geol. Soc. America Bull. 84: 2957-2980.

Peck, D. L., A. B. Griggs, H. G. Schlicker, F. G. Wells, and H. M. Dole. 1964. Geology of the Central and Northern Parts of the Western Cascade Range in Oregon. U.S. Geol. Survey Prof. Paper 449. 56 p.

Received March 1, 1974.

Accepted for publication November 24, 1974.

Tim W. Clark

Department of Zoology
University of Wisconsin
Madison, Wisconsin

Body Measurements of Western Jumping Mice from Northwestern Wyoming

Abstract

The ecology of the western jumping mouse (*Zapus princeps utahensis*) was investigated by Clark (1971) in Grand Teton National Park, Wyoming. In conjunction with that study, body measurements were made on 115 mice. This paper reports those data (Table 1).

The only previously published morphological data on *Z. p. utahensis* from Wyoming were by Long (1965). He listed average and extreme external measurements of 16 adults (7 males) as follows: total length, 246.1 mm (228-268 mm); length of tail, 145.6 mm (131-165 mm); hind foot, 33.5 mm (31-35 mm); ear from notch, 15.3 mm (13-17 mm). His specimens come from Robertson, Uinta County, about 250 miles south of Grand Teton National Park, Teton County. In all cases Long's measurements are considerably larger than those taken on mice from Teton County. In a series of measurements of *Zapus princeps,* Krutzsch (1954) noted that external dimensions as a whole decrease from north to south: *Z. p. utahensis* is the largest subspecies and occupies an area near the center of the geographic range for the species. Compared with Long's, my data show a reverse trend, with larger mice in the southern part of the range.

Literature Cited

Clark, T. W. 1971. Ecology of the western jumping mouse in Grand Teton National Park, Wyoming. Northwest Sci. 45: 229-238.

Krutzsch, P. H. 1954. North American jumping mice (genus *Zapus*). Univ. Kansas Publ. Mus. Natur. Hist. 7: 349-372.

Long, C. A. 1965. The mammals of Wyoming. Univ. Kansas Publ. Mus. Natur. Hist. 14: 493-758.

Received October 17, 1974.
Accepted for publication November 19, 1974.

TABLE 1. Body measurements of 115 western jumping mice for bimonthly periods throughout 1968 and 1969 annual activity cycle, Grand Teton National Park, Wyoming.

Period and Sex	Body Weight (gms) $\bar{X}$ S.D. (Range)	Total Length (mm) $\bar{X}$ S.D. (Range)	Tail Length (mm) $\bar{X}$ S.D. (Range)	Ear Length (mm) $\bar{X}$ S.D. (Range)	Hind Foot (mm) $\bar{X}$ S.D. (Range)
May 24-31					
♂ (N=18)	23.7±3.1 (19-29)	221.9±27.6 (215-250)	131.2±14.1 (127-148)	15.5±1.2 (13-17)	30.5±1.3 (28-33)
♀ (N=2)	24.0±3.4 (21-27)	246.0±19.8 (232-260)	140.0±11.3 (132-148)	16.0 — ——	31.5±1.0 (31-32)
June 1-15					
♂ (N=11)	22.3±2.5 (19-26)	225.8±10.6 (218-240)	132.9±7.7 (117-145)	15.0±0.7 (14-16)	30.9±1.1 (29-33)
♀ (N=4)	24.5±7.7 (20-36)	224.6± 6.1 (218-230)	134.3±4.1 (130-138)	14.7±1.6 (13-16)	31.0±1.6 (29-32)
June 16-30					
♂ (N=25)	23.3±3.9 (19-37)	225.3±8.7 (216-238)	130.4±5.8 (122-147)	14.9±1.2 (13-16)	30.9±1.2 (29-32)
♀ (N=29)	25.8±4.7 (18-30)	229.6±6.8 (226-239)	133.8±6.0 (130-146)	14.6±0.1 (14-16)	31.1±1.2 (30-33)
July 1-15					
♂ (N=10)	23.0±2.3 (21-25)	220.7±14.2 (204-233)	130.0±13.7 (112-141)	14.5±1.3 (13-16)	29.7±2.5 (27-33)
♀ (N=14)	27.8±4.7 (24-37)	231.0±14.9 (214-245)	134.5±13.8 (124-147)	14.7±1.5 (13-16)	30.2±2.0 (30-33)
July 16-31					
♂ (N=0)	— — —	— — —	— — —	— — —	— — —
♀ (N=2)	24.0±1.0 (23-25)	222.0±8.4 (216-228)	132.0±8.4 (126-138)	15.0±1.0 (14-16)	31.0±1.9 (29-33)

Tim W. Clark

Department of Zoology
University of Wisconsin
Madison, Wisconsin

Ecological Notes on Deer Mice in Grand Teton National Park, Wyoming

Abstract

Habitat affinities, food uses, and reproductive data are presented and discussed for 44 deer mice (*Peromyscus maniculatus artemisiae*) from Grand Teton National Park, Wyoming.

Introduction

In a survey of the small mammal communities of Grand Teton National Park some data were gathered on 44 deer mice (*Peromyscus maniculatus artemisiae*). This paper presents information on occupancy of plant communities, food uses, and reproduction. Other members of the small mammal complex have already been reported on (Clark, 1971a, 1971b, 1973a, 1973b).

Methods

Small-mammal trapping was conducted from June to July, 1968, and from May to July, 1969. The proportion of live and snap traps was uniform among the six plant communities trapped: trapping procedures are detailed by Clark (1973b). The six lowland plant communities trapped to determine habitat affinities are described by Clark (1971a) and Reed (1952). Examination of stomach contents follows Clark (1971a), and checks of reproductive status are after Clark (1973b).

Results and Discussion

Habitat affinities were based on the plant community in which capture was greatest per species (Maxell and Brown, 1968). Only three communities yielded deer mice and 99 percent of these mice were trapped in two communities (Table 1). Both these communities containing numerous deer mice possessed woody overstory vegetation and were the driest stages of the hydrosere succession represented by the six communities. The other four communities frequently contained standing water of varying depths.

In the Great Basin Divide of central Wyoming, Maxell (1973) found deer mice most abundant in the shrub-grass communities where vegetative cover exceeded 40 percent. Deer mice, according to his study, seemed to be limited only by the presence of other rodents in high numbers. The four communities not yielding deer mice contained high numbers of microtines (Clark, 1973b). In the high plains of eastern Wyoming, Maxell and Brown (1968) found deer mice in large numbers in the mountain mahogany-juniper grass community type. In the Beartooth Mountains of Wyoming

TABLE 1. Deer mouse distribution in relation to plant communities in Grand Teton National Park, Wyoming.

Plant Community	Trap Days	No. Mice Caught (Capture per 100 trap days)
Sedge-Meadow	1,704	0 (0.0)
Sedge-Grass Meadow	1,595	0 (0.0)
Shrub-Swamp	1,380	0 (0.0)
Shrub-Sedge-Grass-Savanna	1,653	1 (0.1)
Lowland Aspen	2,071	33 (1.6)
Big Sagebrush	1,633	10 (0.6)
Totals	10,036	44 (0.4)

and Montana, Pattie and Verbeek (1967) found deer mice inhabiting krummholz, rock stripes, fellfield, and dry meadow in decreasing order of preference. In northern Wisconsin, Clark (1972) found that deer mice significantly preferred moderate woody cover and that no deer mice were trapped from wet soil areas.

Deer mice were omnivorous (Table 2). The majority of identifiable material was

TABLE 2. Stomach contents of 39 deer mice in Grand Teton National Park, Wyoming. Figures are mean volumetric estimates calculated to the nearest 1 percent. Figures in parentheses are percent frequencies of occurrence.

Stomach Contents	Volumetric Estimates	(Percent Frequencies)
Green Plant Materials	3.0	(8.0)
Seed Fragments	7.0	(2.0)
Arthropods	48.0	(80.0)
Other Animal Tissue	8.0	(15.0)
Unidentified	33.0	(100.0)

animal matter (56 percent), showing the predominant carnivorous component of deer mice diet. Plant materials represented 10 percent and 33 percent was unidentifiable.

Food habits of deer mice from other studies and areas show the mice to be clearly omnivorous. Analyses by Williams (1955) of 125 mice from Colorado forests showed that in July, arthropod remains constituted 80 percent of stomach contents by volume, but seeds made up only 15 percent. These values compare favorably with estimates of food uses in my study. Williams (1959) examined stomach contents of 122 deer mice from Wyoming and Colorado, some of them taken in the forests of regions in my study area: seeds were the major food item (33-79 percent) in all deer mice trapped in Wyoming. Arthropods comprised 8-28 percent of the total diet. These estimates of stomach contents contrast with deer mice diets in northern Wisconsin (Clark, 1972): deer mice (N=20) diet was made up of green plants (47 percent) and seeds (44 percent).

Reproductive status was determined for all the adults (N=23) captured. Only one of the 14 males examined had abdominal testes; the rest were scrotal (Table 3). Limited sample sizes did not provide a basis for detailed accounts of trends in reproductive characteristics. However, changes in testis lengths and weights tended to correspond with those of seminal vesicle lengths and weights. Of females (N=9) only four were found to be pregnant, and the mean litter size based on embryo counts was 6.2 (range 4-7).

TABLE 3. Reproductive status of 13 male deer mice from Grand Teton National Park, Wyoming.

Reproductive Parameter	Period							
	24-31 May (N=1)		1-15 June (N=7)		16-30 June (N=4)		1-15 July (N=1)	
	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
Testis Lengths (mm)	10	—	10.8	(10-11)	8.5	(5-10)	10	—
Testis Weights (mg)	0.390	—	0.384	(0.330-0.502)	0.318	(0.078-0.369)	0.412	—
Seminal Vesicle Lengths (mm)	11	—	14.9	(13-17)	14.0	(11-17)	15.0	—
Seminal Vesicle Weights (mg)	0.170	—	0.253	(0.210-0.402)	0.231	(0.126-0.405)	0.391	—

Long (1964) lists reproductive records of seven *P. m. artemisiae* from northwestern Wyoming and records the mean litter size based on embryos from five females as 6.0 (range 5-7). Reproduction in *P. m. nebrascensis* was studied in the Laramie Basin of Wyoming by Brown (1966). He found adult females in breeding condition from April to August each year: the overall mean number of *corpora lutea* per breeding female was 5.77 ± 0.46, and embryos averaged 5.31 ± 0.49. Maxell (1973) found a mean embryo size of 5.5 (range 4-8) in the Great Divide Basin of Wyoming.

Literature Cited

Brown, L. N. 1966. Reproduction of *Peromyscus maniculatus* in the Laramie Basin of Wyoming. Amer. Middl. Nat. 76: 183-189.

Clark, T. W. 1971a. Ecology of the western jumping mouse in Grand Teton National Park, Wyoming. Northwest Sci. 45: 229-238.

———. 1971b. Aberrant coloration in *Microtus pennsylvanicus* from Grand Teton, National Park. Northwest Sci. 45: 227-228.

———. 1972. An ecological survey of the mammals of northcentral Wisconsin. Mus. Nat. Hist., Rept. Fauna and Flora of Wisc., No. 8: 1-36.

———. 1973a. Distribution and reproduction of shrews in Grand Teton National Park, Wyoming. Northwest Sci. 47: 128-131.

———. 1973b. Local distribution and interspecies interactions in microtines, Grand Teton National Park, Wyoming. Great Basin Nat. 33: 205-217.

Long, C. A. 1964. Comments on reproduction in the deer mouse of Wyoming. Trans. Kan. Acad. Sci. 67: 149-153.

Maxell, M. H., and L. N. Brown. 1968. Ecological distributions of rodents on the high plains of eastern Wyoming. Southwestern Nat. 13: 143-158.

Maxell, M. H. 1973. Rodent Ecology and Pronghorn Energy Relations in the Great Divide Basin of Wyoming. Ph.D. thesis. Univ. Wyo. 208 p.

Pattie, D. L., and N. A. M. Verbeek. 1967. Alpine mammals of the Beartooth Mountains. Northwest Sci. 41: 110-117.

Reed, J. E. 1952. The vegetation of Jackson Hole Wildlife Park, Wyoming. Amer. Midl. Nat. 48: 700-729.

Williams, O. 1955. The food of mice and shrews in Colorado montane forests. Univ. Colo. Studies, Biol. Ser. No. 3: 109-114.

———. 1959. Food habits of the deer mouse. J. Mammal. 40: 415-419.

Received October 17, 1974.
Accepted for publication November 19, 1974.

M. Fareed
and
M. M. Caldwell

Department of Range Science and the Ecology Center
Utah State University
Logan, Utah

Phenological Patterns of Two Alpine Tundra Plant Populations on Niwot Ridge, Colorado

Abstract

Inclined point quadrats were used to quantify phenological development of plant populations growing in an alpine tundra *Kobresia* meadow and a *Deschampsia* meadow during the summer of 1971 on Niwot Ridge, Colorado. These measurements suggest that variations in phenological patterns in the two sites may be related to differences in the duration of snow cover and surface meltwater. Snow melted from the *Kobresia* site 20 days earlier than from the *Deschampsia* site. Signs of dormancy were noted earlier in the *Kobresia* site plants, and the duration of fruit development was generally shorter than that observed in the *Deschampsia* community. Many plants in both sites remained vegetative throughout the season, while others completed only a portion of the reproductive cycle. Harsh alpine environmental conditions of the current season and/or of the previous season may be related to this lack of reproductive development.

Introduction

Strategies for plant survival in the harsh alpine environment hinge critically on the timing and duration of phenological stages during the short growing season. This is complicated by microsite variability and the vicissitudes of weather in the alpine tundra. This study characterizes phenological development in two alpine tundra plant communities in a saddle area of Niwot Ridge, Colorado. These communities are representative of community types of mesic to xeric conditions in the alpine region of the Eastern Slope of the Rocky Mountains.

Accumulation of snow, time of snow melt, and persistence of meltwater were the primary physical factors which differed in the two communities. Phenological sampling was conducted on a population basis so as to represent adequately microsite variability within each community.

Description of Area

The two major alpine community types examined here are located on a gently sloping saddle of Niwot Ridge, Colorado (40°40′N, 105°36′W, 3476 m elevation).

The *Kobresia* site has a southwest aspect and a 5° slope and is typical of a well developed, mesic meadow which can be snow-free for up to 250 days per year. The dominant species, *Kobresia myosuroides* (Vill.) Fiori & Paol., is associated with *Geum rossii* (R. Br.) Ser., *Trifolium parryi* Gray, and *Polygonum bistortoides* Purch. A total of 15 species were contacted in the *Kobresia* site.

The *Deschampsia* site is characteristic of areas where snow cover may persist until late June and where meltwater runoff is heavy. This site has a southeast aspect and a 4° slope. Because of its location on the saddle, the *Deschampsia* site is some-

what less exposed to wind than the *Kobresia* site, and snow accumulates to greater depths. Only 67 snow-free days per year were observed in this site in 1970 to 1971 (Ebert, unpublished data). Here, *Deschampsia caespitosa* (L.) Beauv. is commonly found with *Artemisia scopulorum* Gray and *Geum rossii.* The *Deschampsia* meadow is characterized by only 16 species, 11 of which also occur in the *Kobresia* site.

Figure 1 shows daily radiation, precipitation, and temperature for the 1971 growing season measured at the D-1 experimental site on Niwot Ridge. Climatic data were provided by the Institute of Arctic and Alpine Research, University of Colorado, Boulder. The relationship of the D-1 and saddle area sites is described by Marr (1967). The two areas on the ridge are climatically very similar (Clark, unpublished data).

Methods

Modified inclined point quadrats as described by Warren Wilson (1960) were used to measure phenology of plants on a population basis throughout the 1971 growing season for each species in the two communities. In each of ten plots, 47 point quadrats were placed at horizontal intervals of 2 cm and were passed through the low growing vegetation at an inclination of 32.5°. Sampling occurred at ten-day intervals between late June and late August.

For every plant contacted by the inclined point frame, the most advanced phenological stage was recorded. For example, if a plant were breaking bud and flowering at the same time, then it was categorized as being in the flowering stage.

A voucher collection of all species is on file with the Intermountain Herbarium, Logan, Utah.

Results

Quantitative indices of the phenology status of dominant species in the two alpine sites are given in Figure 2. The duration of snow cover varied in the two sites. Snow melted from the *Kobresia* meadow between May 25 and June 1, 1971, but not until June 15-20 from the *Deschampsia* site. Most of the *Deschampsia* meadow was saturated by meltwater from snow at higher positions on the same slope until late June.

A range of 150 to 600 plants were sampled on each date in the *Kobresia* site. The *Deschampsia* site community sample consisted of 90 to 300 plants on each sampling date. In both sites, the sample size decreased towards the end of the growing season. Because *Kobresia myosuroides* often reproduces by tillering, differentiating individual plants was occasionally difficult. Most clumps of *Kobresia* were treated as separate plants.

A few species in each site had formed buds and flowers by the first sampling date. In both sites, *Geum rossii* was in bud and in the *Kobresia* site, *Carex rupestris* All. and *C. scopulorum* Holm were in flower. In the *Deschampsia* site, *Artemisia scopulorum* and *Caltha leptosepalla* DC., a minor component of the community, had reached the flower stage by the first sampling date.

Within each site, species varied in the time of onset and the duration of phenological stages. *Geum rossii* plants in the *Kobresia* site tended to form buds, flowers, and fruits earlier than other species in this site. Fruiting began about June 25 and continued for 50 days. In the *Deschampsia* site, *Artemisia scopulorum* and

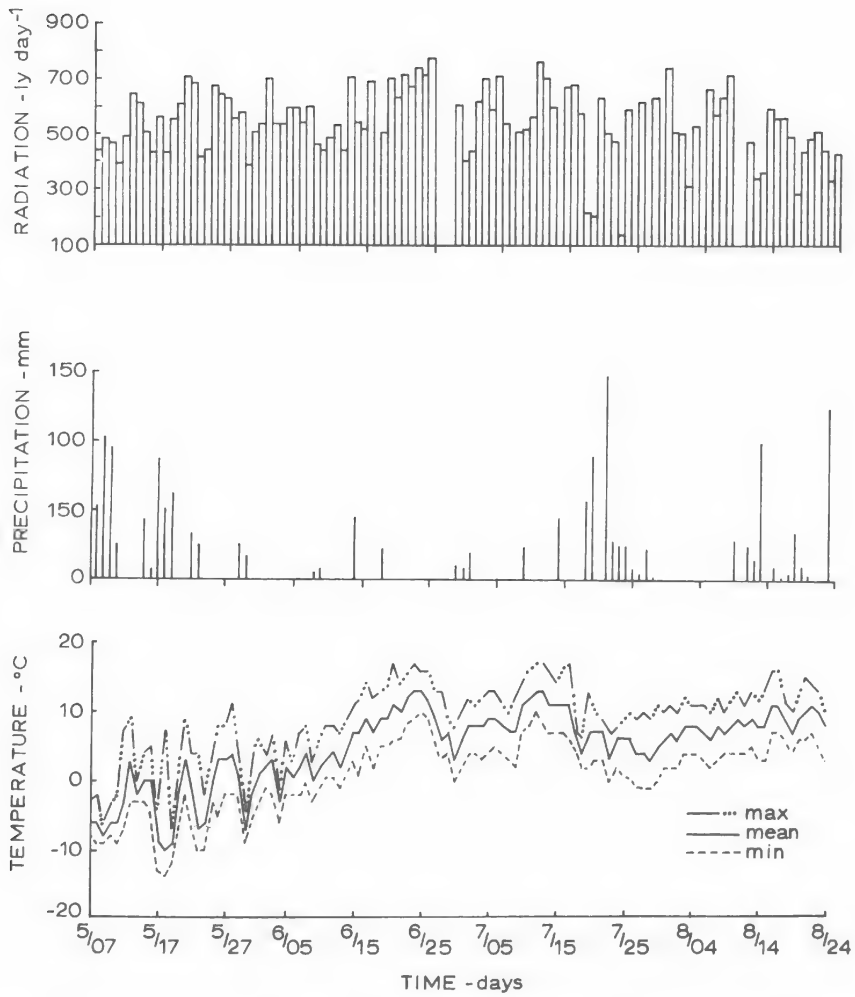


Figure 1. Daily radiation, precipitation, and temperature on Niwot Ridge (3727 m), Colorado from May through September, 1971. No radiation data were available for the following dates: 6/17, 6/26, 6/27, 6/28, 7/7, 8/9, and 8/10 (climatic data for Niwot Ridge D-1 station provided through the Institute of Arctic and Alpine Research, University of Colorado, Boulder).

Deschampsia caespitosa began fruit formation about July 15 and continued fruit production for 30 days. Similarly, in the *Kobresia* site, *Polygonum bistortoides* and *Kobresia myosuroides* first formed fruit on July 15. This stage persisted for 30 days in *Polygonum* and for 40 days in *Kobresia.*

When the two communities are compared in terms of total foliage, the duration of phenological stages appears quite similar, although snow melted from the *Kobresia* meadow about 20 days before it did from the *Deschampsia* site. Bud stage began before sampling and continued for nearly 40 days. Flowering also began before sam-

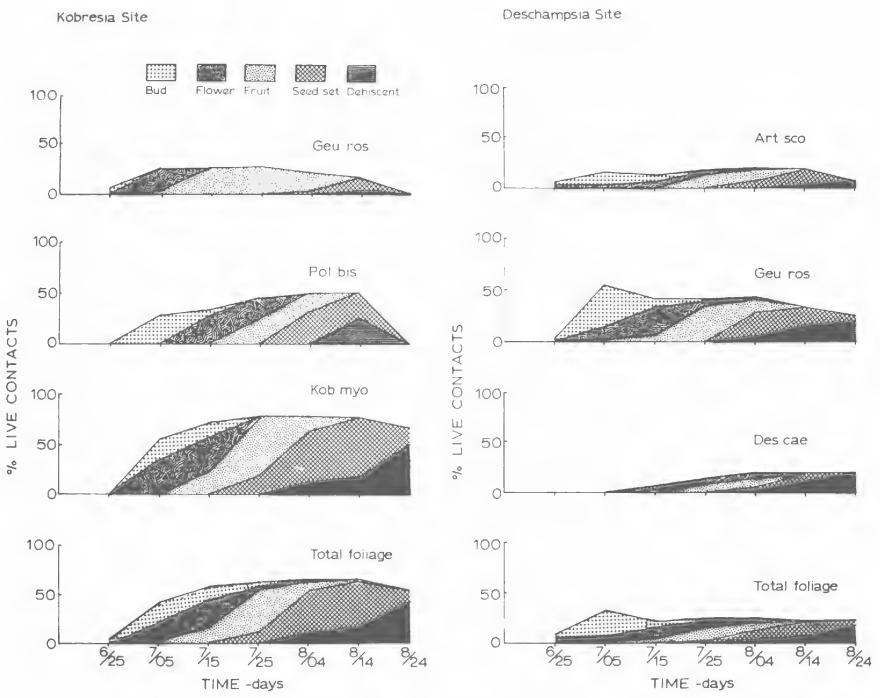


Figure 2. Phenological strips for selected species in the *Kobresia* site (*Geum rossii, Polygonum bistortoides, Kobresia myosuroides,* and total foliage) and the *Deschampsia* site (*Artemisia scopulorum, Geum rossii, Deschampsia caespitosa,* and total foliage) on Niwot Ridge during the summer of 1971.

pling in the two sites and persisted approximately 50 days. Fruit development was first observed on July 5 in both sites. In the *Kobresia* site, fruiting continued for approximately 50 days. In the *Deschampsia* site, the fruiting stage was extended at least ten days longer than in the *Kobresia* site. Seed set was first observed on July 15 in both sites, and seed set was still active on the last day of sampling. Dehiscence of seeds extended from approximately July 25 through the last sampling date.

Based on the percent of quadrat contacts, the *Deschampsia* site had a greater proportion of plant material which was in a vegetative state on all sampling dates. On August 25, 75 percent of the *Deschampsia* site contacts, as compared to 41 percent in the *Kobresia* site, were vegetative.

Indications of dormancy were first observed in the *Kobresia* site in early August, when leaves of *Geum rossii* showed an increase in apparent anthocyanin content. In the *Deschampsia* site, signs of dormancy did not appear until late August, when *Artemisia scopulorum* and *Geum rossii* were the first species to show signs of senescence.

Discussion

The *Deschampsia* and *Kobresia* communities exhibited similar timing and duration of phenological stages. Yet, differences in phenological patterns appeared when species common to both communities were examined. *Deschampsia caespitosa* showed

variation in the initiation and duration of phenological phases at the two sites. Seed set began ten days earlier in the *Kobresia* site and lasted two weeks longer than the same stage in the *Deschampsia* site. There was at least a ten-day lag in the onset of the flower, fruit, seed set, and dehiscent stages of *Polygonum bistortoides* in the *Deschampsia* site, compared to the *Kobresia* site population. *Geum rossii* varied in the duration of bud and flower stages and in the time of initiation of dehiscence. Both bud and flower stages were completed earlier than the same stages in the *Deschampsia* site.

The observed variation in both the time of initiation and the duration of stages in a given species occurring in the two sites is in some contrast with the findings of Holway and Ward (1965). They found that, for a given species, the time of initiation for a phenological phase could vary considerably from site to site; yet, the duration of phases generally showed little variation within an alpine species.

Although plant phenology responds to an interacting complex of physical factors such as air temperature, precipitation, irradiation, soil temperature, and soil moisture content, as well as to community structure and competition, some abiotic factors appear to be particularly well correlated with phenological progression. Reproductive events of the phenological cycle are correlated to a greater extent with air temperature than with either precipitation or irradiation. The rise in air temperature during late May and early June paralleled the development of reproductive buds and flowering in both the *Kobresia* and the *Deschampsia* sites. Maximum mean daily air temperatures occurred between June 15 and July 17 when bud development, flowering, and fruit stages had all been initiated. A cooling trend, marked by occasional below-zero minimum temperatures, began on July 17, which was also the time of initiation of the seed set stage in both sites.

Soil temperature and moisture status may also be related to specific phenological events. Figure 3 shows average soil moisture and temperature data for the two Niwot Ridge study areas. In the *Deschampsia* site, a considerable increase in the fruit production of all species occurred approximately July 15, the date when average soil moisture began to decrease. Plants of *Geum rossii* in the *Kobresia* site (early snow release) exhibited changes in pigmentation approximately 20 days before plants of the same species in the *Deschampsia* site (late snow release). When dormancy was first observed in the *Kobresia* site in early August, the soil moisture was approximately 10 percent by weight lower than in the *Deschampsia* site.

In 1972, snow melt occurred approximately 18 days earlier in the *Kobresia* meadow than in the *Deschampsia* site, in a pattern similar to 1971. Leaf relative growth rate and photosynthetic capacity measurements of *Geum rossii* in the two sites indicated a much earlier curtailment of growth and photosynthesis in the *Kobresia* site (Johnson and Caldwell, 1974). This shift in photosynthetic capacity and growth rates between the two sites in 1972 is in some respects comparable to the shift in phenological progression based on reproductive organs; however, the shift between the two sites is not linear for all phenological stages. Instead, there is telescoping of the sequence of phenological stages of *Geum* in the *Deschampsia* site. This would seem to be beneficial in accommodating the less favorable weather patterns towards the termination of the growing season which would, of course, occur at about the same time for both sites.

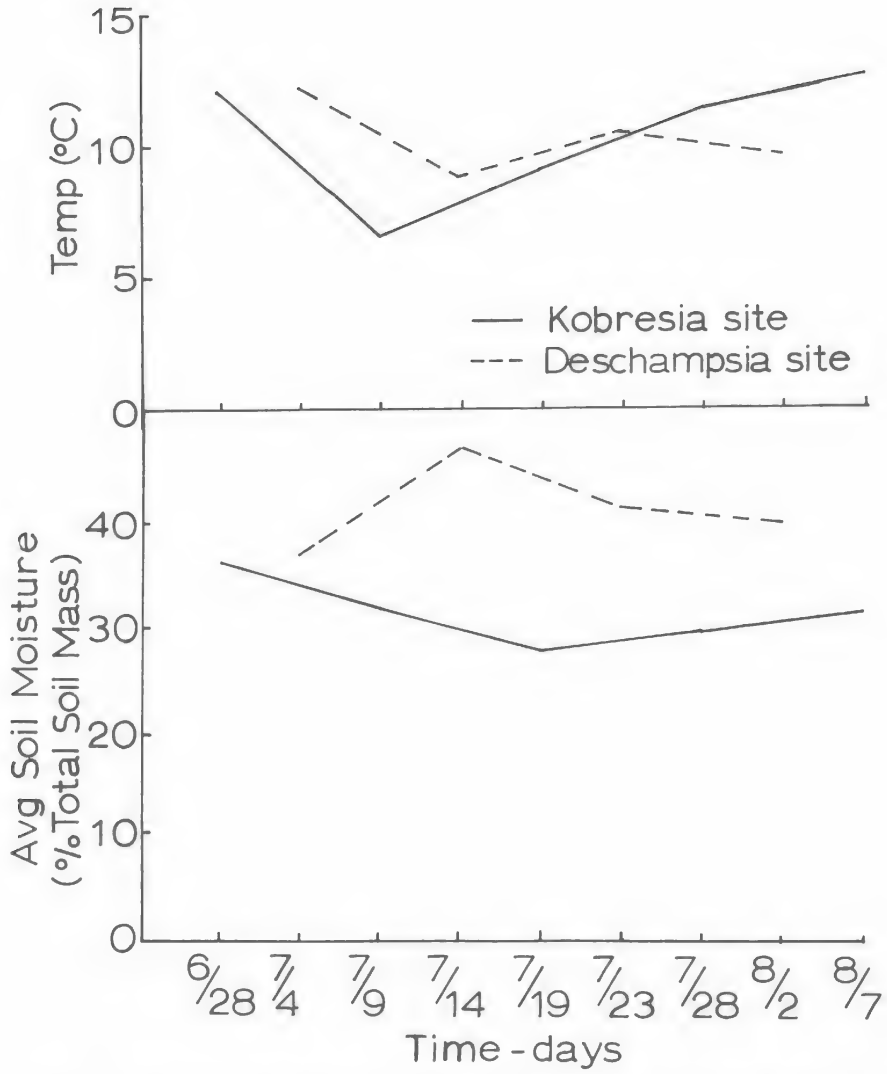


Figure 3. Soil temperature at a depth of 7.5 cm and average soil moisture for the *Kobresia* (solid line) and *Deschampsia* (dashed line) sites during 1971 (unpublished data, personal communication, Paul Gersper).

The large number of species which remained vegetative can be explained, in part, by the severe alpine environment. In the most severe environments, sexual reproduction decreases and becomes variable and unreliable, while vegetative reproduction in the form of apomixis, vivipary, and rhizomes is important for most tundra species (Billings and Mooney, 1968). Holch *et al.* (1941) noted that many alpine perennials reproduce vegetatively because the short alpine growing season is prohibitive to seed set. The greater proportion of plants which remained vegetative in the

Deschampsia site may be a reflection of the delayed timing of snow melt, resulting in a somewhat shorter growing season than occurred in the *Kobresia* site. Possibly, yearly variations in the severity of the alpine weather would also be reflected in the amount of vegetative reproduction.

The two communities depicted in this study appear to differ primarily in the length of time under snow, in the dates of snow melt in the spring, and in average soil moisture. These differences seem to be clearly reflected in the phenological progression of the principal species. For species common to both sites, telescoping of phenological events is apparent. In the *Deschampsia* site, where the duration of snow cover was greater and where snow melt occurred later in the spring, a greater number of plants remained vegetative throughout the growing season.

Acknowledgements

This work was financially supported by National Science Foundation Grant GU-29353X1 to M. M. Caldwell and L. L. Tieszen. Thomas Shoemaker, Roger Hanson, and Diane Hanson provided field assistance in this study. Support provided by the Institute of Arctic and Alpine Research, University of Colorado, and the I.B.P. Tundra Biome Center, University of Alaska is also gratefully acknowledged.

Literature Cited

Billings, W. D., and H. A. Mooney. 1968. The ecology of arctic and alpine plants. Biol. Rev. 43: 481-529.

Holch, A. E., E. W. Hertel, W. D. Oakes, and H. H. Whitwell. 1941. Root habits of certain alpine plants of the foothills and alpine belts of the Rocky Mountain National Park. Ecol. Monog. 11(2): 327-345.

Holway, J. G., and R. T. Ward. 1965. Phenology of alpine plants in Northern Colorado. Ecology 46: 73-83.

Johnson, D. A., and M. M. Caldwell. 1974. Field measurements of photosynthesis and leaf growth rates of three alpine plant species. Arc. and Alp. Res. 6: 245-251.

Marr, J. W. 1967. Ecosystems of the East Slope of the Front Range in Colorado. Univ. Colo. Studies, Series No. 8, Univ. Colo. Press, Boulder, Colo. 134 pp.

Warren Wilson, J. 1960. Inclined point quadrats. New Phytol. 59: 1-8.

Received March 4, 1974.
Accepted for publication November 19, 1974.

R. Daubenmire

Department of Botany
Washington State University
Pullman, Washington

Ecology of Artemisia tridentata subsp. tridentata in the State of Washington

Abstract

The ecological amplitude of *Artemisia tridentata* subsp. *tridentata* is broad enough to allow it to occur naturally in arid climates ranging from those with precipitation mostly in winter, as in the state of Washington, to those with precipitation mostly in summer, as in New Mexico. Autecologic and synecologic characters of this shrub as it is represented in a winter-wet climate are presented. These characters include reproduction and stand formation, rooting pattern of established plants, phenology and water relations, weather and xylem increments, influence upon associated plants, age-class distribution, and size-class distribution.

Artemisia tridentata Nutt. subsp. *tridentata* is a widespread shrub in the steppes of western North America (Beetle, 1960). It has been well studied morphologically (Diettert, 1938), and much has been written regarding its significance for range management, but relatively little has been published regarding its autecology. The subspecies is so widely distributed that considerable genetic differentiation must exist to enable it to fit into very diverse climatic regimes (Fig. 1). This account reviews ecologic information on the shrub as it occurs in Washington, drawing on material in unpublished theses and adding data gathered by the writer.

Reproduction and Stand Formation

Studies of seed production and ecology have been made by Goodwin (1956). He found that disseminules, i.e., achenes enveloped in their adhering calyx tube, as collected on Pleasant Ridge in Asotin County, varied in average weight from 0.17 mg to 0.24 mg per hundred. Fibers remaining attached to the calyx tube, where it breaks away from the rest of the corolla, give the structure much of the character of a small bur and account for the manner in which it readily adheres to mammalian fur.

A plant having a canopy approximately 1 m broad and growing on shallow, rocky soil had 450 inflorescences and was estimated to have produced 335,000 seeds. Each head produced an average of 2.47 florets. A nearby plant on deep loam produced an average of 4.6 florets per head and so probably produced twice as many seeds.

Dissemination occurred in mid-November on Pleasant Ridge. In general, the more moist the site, the later the dissemination. Seedlings appeared on bare ground as far as 33 m from possible parent plants, suggesting that wind dissemination is also effective.

Stratification was unnecessary for germination, but it gave a higher total and

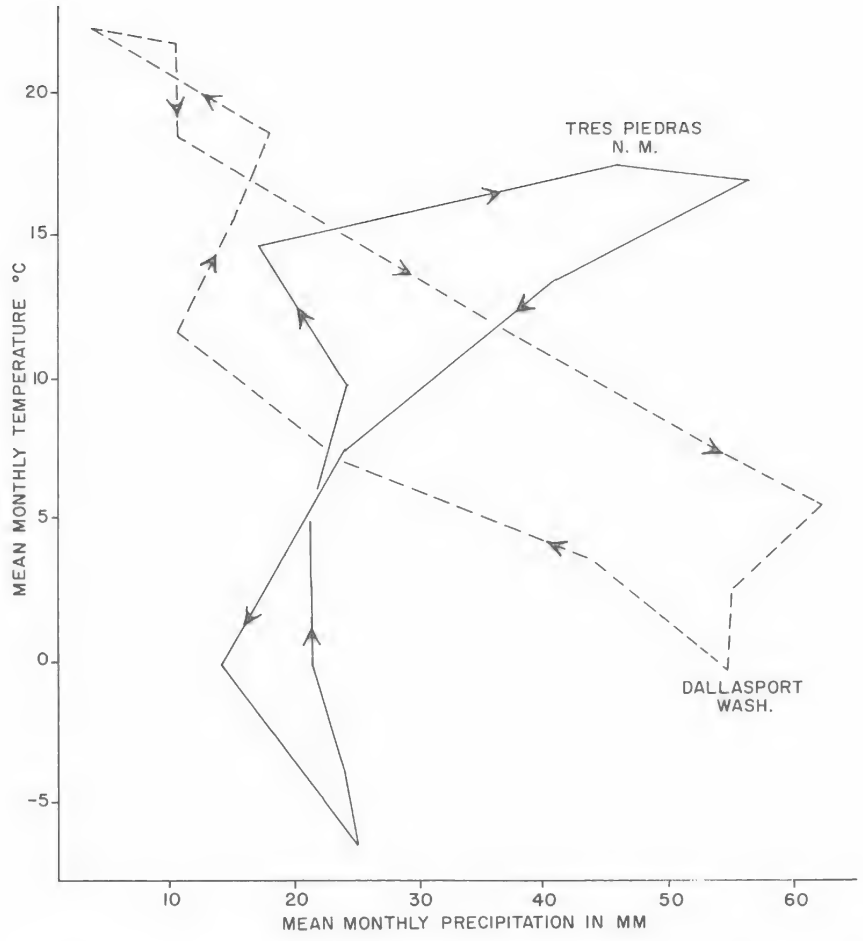


Figure 1. Progressive changes in mean monthly temperature and precipitation through the year at two locations in the range of *Artemisia tridentata* ssp. *tridentata.*

more prompt germination. Seed germinated better in light than in darkness but did not germinate during stratification periods up to 40 days. Maximum germination in the laboratory was 90 percent. Disseminules which were floated on water for 30 days had a 22-45 percent germination in different tests. Submersion under water yielded slightly higher germination. Contact with free water is essential for good germination, and temperatures must be cool, at least at night. Germination occurs naturally in midwinter when the soil is wet but subject to nocturnal freezing. At the Asotin County site germination continued from February 7 to April 4, but some viable seeds were left after natural germination stopped.

Primary leaves appear six weeks after the cotyledons expand. The tap roots of the seedlings elongate at the rate of 0.7-0.8 mm/24 hrs under field conditions. This

growth is much slower than the root growth of associated annuals and perennials. Shoot development is very slow in spring while the tap root is elongating, with only 22 m of epicotyl developed by May 8. Seedlings can endure saturated soil for up to three weeks, but few survive for as long as four days after soil moisture about their roots declines to the permanent wilting percentage. In the first summer seedlings grew up to 50 mm in height. Seedlings may reach the flowering stage in three years.

Rooting Pattern of Established Plants

The pattern of root systems in a silt loam near Richland was studied by Price (1965). He placed limited quantities of water-dissolved iodine-131 at recorded depths in the soil, then examined plants at varying distances from these sites to see which had taken up the isotope and must therefore have had roots where the isotope was liberated. Uptake was most vigorous in April.

The depth of the isotope study was limited to a loessal deposit about 1 m thick, that rested on gravel. Within the loam, roots extended up to 3.2 m from the axis of a plant. Plants 60-90 cm tall had longer lateral roots than plants that were shorter or taller.

The pattern of the root system was found to be hour-glass shaped, with one concentration of long laterals centered about the 40-cm depth, and another concentrated at approximately 80 cm (Fig. 2). Some tap roots extended to 3 m, at which depth they encountered basalt bedrock. Shallower penetration was associated with a subsoil of pure sand at another location. Differences in the pattern of root systems could be noted in the three distinctive types of communities in which observations were made.

Only part of a canopy was made radioactive when one root of a plant made contact with an injected spot in the soil. Therefore, leaves from all sides of a plant must be included in the sampling, if a study of this nature is to be definitive.

Later the same technique was used by Rupp (1969) to study roots of plants growing on sand near Richland. The root system of *Artemisia tridentata* was again shown to be hour-glass shaped, with one major horizon of greater lateral extent centered between 50-70 cm and another centered at 120 cm (Fig. 2). In shallow soil the maximum root concentration observable was at 40 cm. The maximum lateral spread of any root was 5.15 m from the axis of the plant, a distance considerably greater than Price found in loess.

Phenology and Water Relations

On Pleasant Ridge, Goodwin (1956) reported that buds on established plants started enlarging April 10, and a week later apical growth was well under way. By June 19 shoots resulting from elongation of apical buds had attained full size, and at this point in development old, overwintering leaves began to be cast, and axillary buds on the new shoots began to develop. Some of these axillary buds developed into short, sterile shoots, others into long, flowering shoots. As the new set of leaves on the sterile side-shoots matured, those on the twig that first elongated were cast. By July 1 flower buds were visible in the axils of the flowering shoots.

At Richland, where the altitude is much lower and the climate warmer, Price (1965) found new leaves being expanded in late March, and continuing their growth

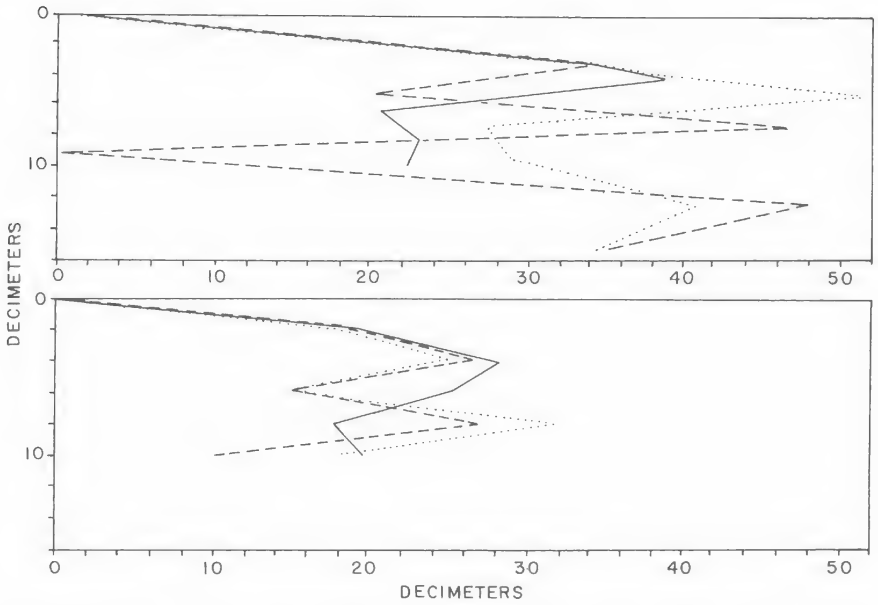


Figure 2. Maximum extent of root systems for plants growing at three locations in sand (above) and three locations in loess (below). The upper left hand corner of each rectangle represents the center of the root-stem transition. (Redrawn from Rupp, 1969, and Price, 1965, respectively.)

until June 1, after which inflorescences began to expand. Overwintering leaves were cast while the inflorescence was developing. Pollination took place in October, before the onset of the winter rainy season. Plants that remained vegetative in the first season of study also failed to produce flowers in the second.

Price found that, on an oven-dry basis, foliage moisture content exceeded 100 percent (to 165 percent) until the end of May, after which it declined, reaching the lowest value (55-60 percent) in August to October. When winter rains began, the water content abruptly doubled, after which there was little increase until the end of February when a further period of rehydration brought the water content once more above the 100 percent level. It was not until this time that the soil moisture recharge was completed, with moisture from the winter rains never penetrating deeper than 50-60 cm. Attainment of minimum leaf moisture content coincided with the exhaustion of the readily available soil moisture that had accumulated during the preceding winter.

On sandy soils and in another year, Rupp (1969) observed leaf moisture content remaining above 100 percent until early July, but then rehydration to this level was delayed until after mid-February. Moisture content of the foliage closely paralleled the alternation of moist and dry states of the soil at a depth of 50 cm, and iodine uptake occurred only when soil moisture and leaf moisture were high.

Phenologic studies relevant to moisture stress were made by the writer using five plants growing in the valley of Alpowa Creek west of Clarkston, Washington. These plants were rooted in loess on the south side of the valley, well above the

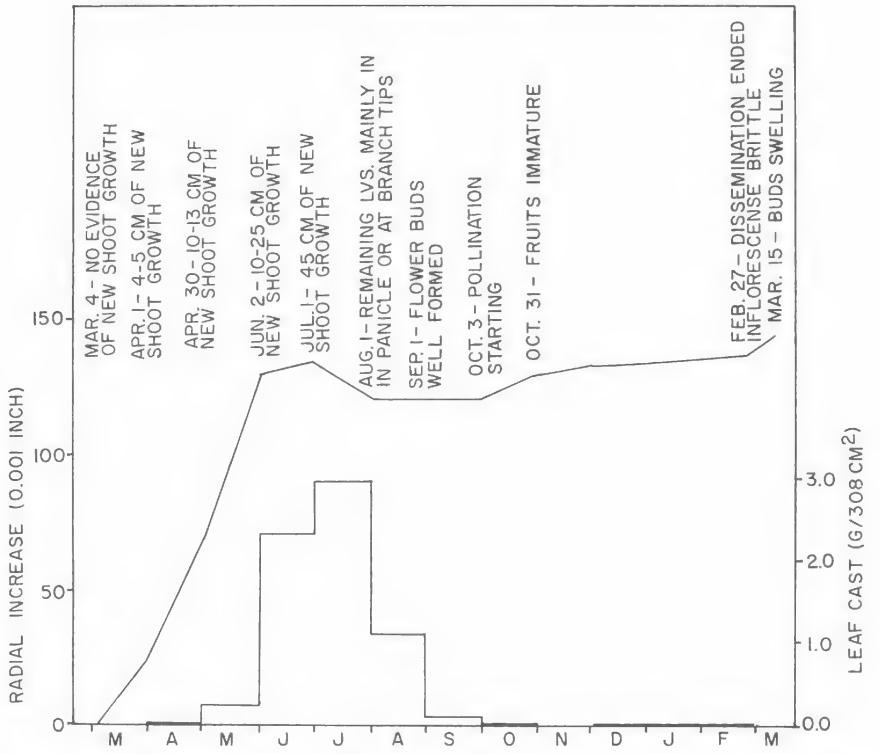

MAR. 4 - NO EVIDENCE OF NEW SHOOT GROWTH
APR. 1 - 4-5 CM. OF NEW SHOOT GROWTH
APR. 30 - 10-13 CM. OF NEW SHOOT GROWTH
JUN. 2 - 10-25 CM. OF NEW SHOOT GROWTH
JUL. 1 - 45 CM. OF NEW SHOOT GROWTH
AUG. 1 - REMAINING LVS. MAINLY IN IN PANICLE OR AT BRANCH TIPS
SEP. 1 - FLOWER BUDS WELL FORMED
OCT. 3 - POLLINATION STARTING
OCT. 31 - FRUITS IMMATURE
FEB. 27 - DISSEMINATION ENDED INFLORESCENSE BRITTLE
MAR. 15 - BUDS SWELLING
RADIAL INCREASE (0.001 INCH)
LEAF CAST (G/308 CM²)
150
100
50
0
3.0
2.0
1.0
0.0
M A M J J A S O N D J F M

Figure 3. Radial changes in stems, leaf cast (histogram), and phenologic notes from 4 March 1972 to 15 March 1973.

influence of a water table in the terrace below. The habitat had been disturbed in the past, and the individuals studied were now meeting competition chiefly from *Sporobolus cryptandrus, Bromus tectorum,* and *Chrysothamnus nauseosus.*

Each bush was provided with a dendrometer (Daubenmire, 1945) which was read at approximately monthly intervals. Under each bush, approximately midway between stem and canopy margin, a can with small drainage holes was set to collect litter. Mean radial changes and air-dry weights of litter are shown, along with phenologic notes in Figure 3.

By interpolation, radial growth commenced on approximately March 7, 1973, and the cluster of immature leaves that constitutes the winter bud began to swell visibly at about the same time. The altitude of this site is approximaely 640 m lower than Goodwin's study site, hence most developmental stages are reached at an earlier date. Cambial growth was very active during March, April, and May, with shoot development progressing steadily during these months. At approximately the beginning of June there was a drastic reduction in the rate of radial increment, followed by pronounced shrinkage in July. This change was probably related to the exhaustion of available soil moisture in the horizons occupied by the upper member of the dual root system. Owing largely to grass activity, soils in the

habitats where *Artemisia* grows dry to a depth exceeding a meter in June (Daubenmire, 1972). Near Richland, Washington, Hinds and Klepper (1974) found the leaf water-potential of *Artemisia tridentata tridentata* remained at approximately –7 bars between March 20 and April 20, after which it decreased, reaching –40 bars by the end of June—a date which coincides with the time shrinkage and heavy leaf-cast begun at Clarkston.

Most of the small winter set of leaves are cast in May as the large summer leaves are produced on the elongating twigs. As these primary twigs bearing large summer leaves approach full size, they give rise to lateral twigs upon which a new set of small winter leaves appear. When the soil dries in the upper horizons, cambial activity ceases, and summer leaves begin to drop. The greatest rate of abscission coincides with the period of stem shrinkage. But despite these evidences of a moisture crisis, the new set of winter leaves persists near the tips of the twigs and in the lower part of the panicles, and inflorescence development continues apace.

As the new xylem layer is developing, the periderm on its adaxial face is likewise developing, and when xylem deposition is completed, the periderm becomes suberized (Diettert, 1938). The moisture crisis resulting in stem shrinkage and rapid abscission apparently follows immediately upon the attainment of the above stage of development.

That the deeper member of the root system gives the plants access to a moisture supply below the reach of grass roots in late summer is shown by (1) cessation of shrinkage after transpiration has been reduced by a shedding of the large summer leaves, with only a reduced mass of smaller leaves remaining functional, and by (2) development leading to flowering and fruiting progressing steadily, with pollination starting before a new supply of moisture is available from autumn rains.

Upon the advent of the winter rainy season, radial shrinkage was eliminated almost completely within a month, after which stem dimensions remained quite stable until the resumption of next season's growth in early March.

Weather and Xylem Increments

In the southerly part of the range of *Artemisia tridentata*, Ferguson (1964) found that the thickness of xylem layers in its stems is correlated with accumulated winter precipitation, November through April, and he hypothesized that a closer relation might be established with soil moisture than with precipitation. To test this hypothesis in Washington duplicate cores of soil divided into decimeter horizons were collected to a depth of 1 m on approximately May 20 over a period of 14 years at Stand 14, as described in Daubenmire, 1970. May 20 was judged to be a propitious date to evaluate moisture stored during the preceding winter. As a means of plotting the data, the moisture content of each year was assigned a rating from 1 to 14, with 1 being the lowest water content of the profile as a whole in any of the 14 years.

On the 14th year, 1969, the trunks of ten shrubs in the same stand were sampled in the spring, and the thickness of their xylem layers was measured along two radii of each stem. At this season the currently accumulating xylem was white, as was the preceding year's accretion, since the 1969 periderm layer on the adaxial surface of the new increment had not yet sealed off the last year's xylem. Xylem increments were measured starting with the inner white increment taken as 1968 growth and progressing backwards.

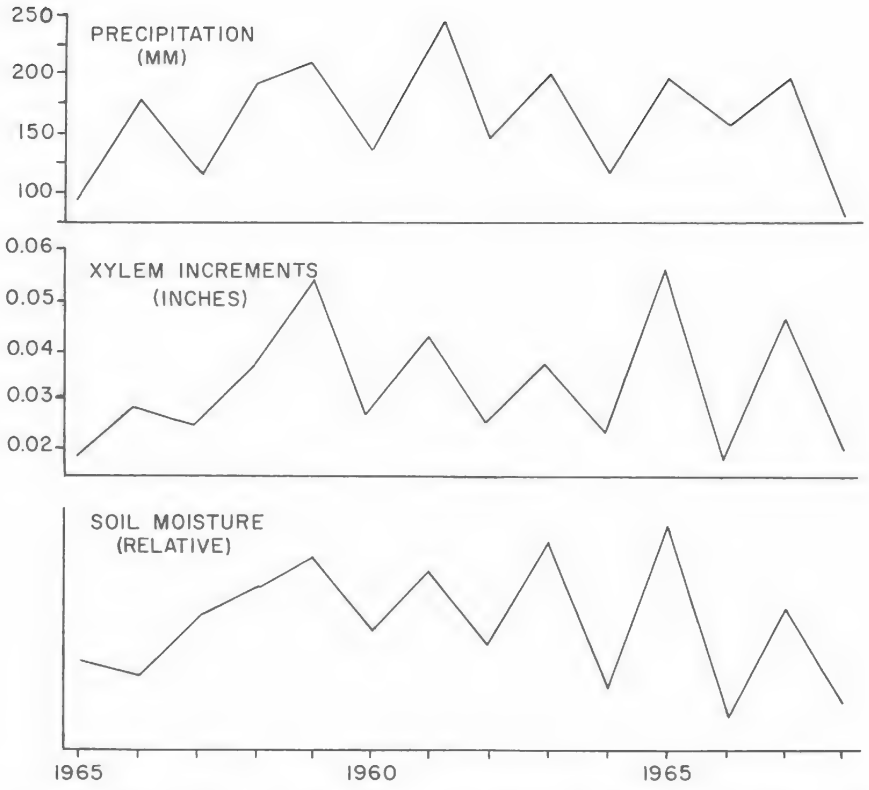


Figure 4. Relation of annual variations in xylem increments to variations in November-June precipitation, and to soil moisture as sampled in late May.

Annual variations in wood increment showed very close agreement among nine of the plants, with one being quite different. The latter was disregarded in averaging the measurements.

Accumulated precipitation from November through April was plotted for data from the nearest weather station (Othello), but since in this summer-dry climate there is a June bulge in the annual precipitation curve, and the cambium is still active in that month, another graph of precipitation was based on the period November through June. The latter graph proved to be a slightly better fit to both the growth and soil-moisture data, and only this graph is included in Figure 4.

Xylem increment in Washington is clearly related to the precipitation accumulating in the moisture year that terminates midway in the period of cambial activity.

There is very good agreement among secondary growth, precipitation, and soil moisture as accumulated in May, with growth more consistently related to the precipitation record, presumably since this includes significant June rainfall.

Relations between *Artemisia* and Plants beneath Its Canopy

The foliage of *Artemisia*, especially when crushed, has an odor suggesting a mixture

of turpentine and camphor, and this might be suspected of possibly representing one or more substances deleterious to associated species. In fact, in the laboratory, Reid (1964) treated seedlings of other species with leaf extracts of *Artemisia tridentata* and, finding the seedlings damaged, concluded that "current investigations indicate that these growth inhibitors may be important in the distribution patterns of at least some species of native grasses." On the other hand, Schlatterer and Tisdale (1970) grew grass seedlings under the influence of *Artemisia tridentata* litter in a glasshouse and found that germination and early growth were somewhat retarded but concluded that "the actual effectiveness of such materials under field conditions is very doubtful."

Field observations in Washington indicate that not only is there no allelopathic influence from this species of *Artemisia*, but that it has a beneficial effect on other plants. All associated species can be found abundantly represented beneath the canopy of *Artemisia,* usually in better-than-average vigor and vitality, and in certain habitats *Poa cusickii* is conspicuously confined to the shaded area (Daubenmire, 1970).

A special relation exists with reference to the alien annual *Bromus tectorum*, which has proven especially well preadapted to the environment of the Washington steppe. Frequently a conspicuous and dense stand of this grass appears beneath each shrub, essentially coinciding in its size with the area of the *Artemisia* canopy above. It is here suggested that this phenomenon is related to the leaf cast of the shrub and to the special significance of the shrub for grasshoppers.

The sum of the leaf litter cast by the Alpowa plants in a year was 7.1959 gm, air-dry, from a combined collecting area of 308 cm^2. Later analysis of the moisture content of the bulked sample indicated a water content of the air-dry litter of 6.7 percent. Assuming that the average of the five samples collected beneath the shrubs approximates the leaf litter cast beneath the entire shrub canopy, this amounts to 218 gm/m^2, oven-dry basis.

The germination of *Bromus tectorum* caryopses is inhibited by light (Hulbert, 1955), and perhaps due to this the plant is favored by a thick litter cover into which the florets can filter when cast. The name *tectorum* (meaning "of the roof tops") suggests its success on thatched roofs in the Middle East, where the plant is native.

Grasshoppers do not eat the foliage of *Artemisia*, but after feeding on green leaves of other plants in the community, they congregate in the canopy of *Artemisia* bushes to roost during the night. Great quantities of their frass had to be separated out of the litter-collecting cans when the leaf material was segregated. Other types of frass were also present but in minor amounts. Such material, presumably high in nitrogen, must undoubtedly favor *Bromus tectorum*, since this species has been shown to be highly responsive to nitrogen applications (Hulbert, 1955).

Thus the effect of litter falling beneath the shrubs to form a mechanically beneficial substrate, combined with the fertilizing effect of the insect frass, must account for many, if not all, of the discs of *Bromus* so commonly observed beneath *Artemisia* canopies. Probably a large part of the favorable influence upon other species growing beneath the *Artemisia* canopy may be attributed to the same rain of litter and frass.

Age-Class Distribution

Since the perennial grasses associated with *Artemisia tridentata* desiccate progressively throughout the rainless summers, fires, when started in mid- or late summer, spread

rapidly through the community. *Artemisia* is readily killed by fire and lacks an ability to sprout from the roots.

In most stands the oldest individuals probably date back to invasion following the last fire to sweep the habitat. Whereas the grass component regenerates from underground organs, *Artemisia* must get established as seedlings in this persistent grass community. In a young burned area adjacent to Stand 28 (Daubenmire, 1970) a plot 4 x 25 m yielded the ages and heights of the eight plants shown in Table 1. Five

TABLE 1. Ages and heights of seedlings of *Artemisia tridentata* in a recent burn adjacent to *Artemisia tridentata-Agropyron spicatum* Stand 28. Plot 4 m x 25 m.

Years	Height (cm)
2	12
5	20.5
6	12
7	7.5
7	15
8	17
9	9
9	15.5

plants of the root-sprouting *Artemisia tripartita* also occurred in this plot, and the new sprouts that arose from their roots had 10, 11, 11, 12, and 12 xylem layers. The age of the burn may thus be estimated as 13 years. If this is correct, *A. tridentata* started to reinvade during the third postfire year, and new plants have been added at a very slow rate. There is no suggestion of origin from seeds cast on the soil prior to the fire, but such young invading plants are capable of producing seeds very shortly. On another burn on Saddle Mountain (southern Grant County) five young plants producing their first flowers were only two years old.

TABLE 2. Numbers and ages of individuals in a 25 (+?)-year old burn in a stand of *Artemisia tridentata-Agropyron spicatum*. Benton County, Washington. Plot 5 m x 5 m.

Years	*Individuals*
17	1
18	1
19	2
20	2
21	6
22	12
23	3
24	4
25	1

Table 2 represents a young *Artemisia* population in a heavy grass cover at the north base of Rattlesnake Mountain, close to Stand 43. The data again show a slow invasion after the last fire, except for the fourth postburn year when nearly half the total population got established. All the plants were branched at the soil surface, and the 3-5 branches had the same age as the tap root just below.

Stand 19 may be considered a modal stand of the *Artemisia tridentata-Agropyron* association in excellent condition (Table 3). The oldest individual, with 95 xylem layers, indicated approximately a century since the last fire. A pronounced modality in the age-class distribution reflects a rarity of conditions favoring seedling success but a substantially high probability of tenure once a plant survives the first critical year.

TABLE 3. Population analyses of *Artemisia tridentata.*

Association		*A. tridentata-Agropyron*	*A. tridentata-Festuca*
Stand No.		19	18
Numbers of individuals by age-classes	1-10	2	15
	11-20	6	73
	21-30	21	4
	31-40	8	1
	41-50	4	
	51-60	2	
	61-70		
	71-80	1	
	81-90		
	91-100	1	
Total		45	93

The complete absence of charcoal and the wide spacing of the older individuals over the heavy grass cover cast doubt on any interpretation of the 21-year to 30-year age class as having had an origin after a partial burn. Likewise, the absence of species favored by grazing would seem to eliminate the possibility of heavy grazing during a short interval allowing a number of *Artemisia* seedlings to become established. The common occurrence of a modal age class in different stands (see also Table 4) probably reflects an unusual concatenation of weather conditions favoring in sequence, seed set, germination, and survival, that occasionally allow each population to approach saturation density rather abruptly. Many hundreds of sample plots scrutinized in detail during spring and summer have shown that most *Artemisia tridentata* seedlings must die before the distinctive cotyledons can be recognized, and of the very few seedlings identified with cotyledons, none survived the first summer. The circumstances indicate that once population saturation is approximated, the establishment of new individuals probably awaits the appearance of a gap resulting from the death of an old plant. The contrast between population structure in *Artemisia tridentata* and that in a type more usually characteristic of a climax species is strikingly illustrated by the inclusion of data representing two stands of *A. tripartita* in Table 4. Stands of the latter species were analyzed in late spring before normal summer mortality, which eliminates many of the youngest of the root sprouts. The phenomenon of a modal age class well above the youngest class is also characteristic of populations of *Artemisia tridentata vaseyana* (Booth, 1951; Harniss and Murray, 1973).

Size-Class Distribution

As *Artemisia tridentata* plants age, stem fission frequently splits the axis to the ground level, with all the several segments continuing normal functions. A strong recurvature of these segments results in a reduction in height after splitting. This at least contributed to the wide disparity between height and age measurements as indicated by comparing the age-class distribution of Stands 18 and 19 in Table 3 with the height-class distribution in Table 4. In the former table there is a strong modality of age; in the latter there is approximately equal representation of individuals having a wide range of height. Table 5 shows that plants no older than 5 years can exceed the height of individuals 16 years of age. Even before stem fission gets under way, height and age tend to have little correlation (Table 1).

TABLE 4. Density by height classes of shrubs per 100 m^2, based on one plot 2 m x 50 m in stands of *Artemisia tridentata* or smaller plots for the vegetatively reproducing *A. tripartita*. Measurements made from ground to tip of highest leaf, with organs in natural positions and inflorescences excluded.

Association	Stand	Species	Decimeter height classes 0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–11	11–12	12–13	13–14	Total
A. tridentata-	7	*A. trid.*	2	6	4	4	5	4	3	4	2	1					10
Agropyron	12	"		3	4	6	9	5	1	3	1	1					33
spicatum	13	"	1	5	11	22	20	21	13	4							97
	19	"		2	3	4	4	5	2	1	1	1					23
	20	"			3	1	1	2	4	2		2	2				17
A. tridentata-	23	"			5	14	17	14	4		5	3	1				63
Stipa comata	11	"		3	12	16	15	8	7	12	3	1	2				79
A. tridentata-	15	"		4	15	18	27	26	21	10	4	1	2				128
Festuca	18	"		3	3	12	12	13	2	1							46
idahoensis																	
A. tripartita-	1	*A. trip.*	430	570	230	220	140	20	20	10							1640
Festuca	2	"	262	317	167	93	33	12									884
idahoensis																	

TABLE 5. Height range within age-classes in *Artemisia tridentata-Festuca.* Stand 18. Plot 5 m x 40 m.

Age–class	No. plants	Height range (cm)
1– 5	1	33
6–10	14	18–50
11–15	52	12–88
16–20	21	21–89
21–25	3	53–78
26–30	1	78
31–35		
36–40	1	58

Acknowledgements

I am indebted to Jean Daubenmire for assistance in most of the field work involved with the original data and to R. F. Harwood for verification of my identification of insect frass.

Literature Cited

Beetle, A. A. 1960. A Study of Sagebrush, the Section *Tridentatae* of *Artemisia.* Wyo. Agric. Exp. Sta. Bul. 368. 83 p.

Booth, W. E. 1951. The effect of grass competition on the growth and reproduction of big sagebrush, *Artemisia tridentata.* Mont. Acad. Sci. Proc. 7: 23-25.

Daubenmire, R. 1945. An improved type of precision dendrometer. Ecol. 26: 97-98.

———. 1970. Steppe Vegetation of Washington. Wash. Agric. Exp. Sta. Tech. Bul. 62. 131 p.

———. 1972. Annual cycles of soil moisture and temperature as related to grass development in the steppe of eastern Washington. Ecol. 53: 419-424.

Diettert, R. A. 1938. The morphology of *Artemisia tridentata.* Lloydia 1: 3-74.

Ferguson, C. W. 1964. Annual Rings in Big Sagebrush, *Artemisia tridentata.* Lab. Tree-Ring Res., Univ. Ariz., Paper 1. 95 p.

Goodwin, D. L. 1956. Autecological Studies of *Artemisia tridentata* Nutt. Ph.D. Thesis, Washington State Univ., Pullman. 72 p.

Harniss, R. O., and R. B. Murray. 1973. Thirty years of vegetal change following burning of sagebrush-grass range. J. Range Man. 26: 322-325.

Hinds, W. T., and B. Klepper. 1974. Sagebrush leaf water potentials in grazed and ungrazed grasslands. Battelle Pacific Northw. Lab., Ann. Rept. for 1973. Part 2: 140-141.

Hulbert, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual brome grasses. Ecol. Mono. 25: 181-213.

Price, R. K. 1965. Uptake of Iodine-131 from the Soil as Related to Root Distribution and Phenology in Sagebrush Vegetation. Ph.D. Thesis, Washington State Univ., Pullman. 85 p.

Reid, A. 1964. Growth inhibitors in shrub species in Wyoming. Ecol. Soc. Am. Bul. 45: 94.

Rupp, M. S. 1969. Root Distribution of *Artemisia tridentata* and *Purshia tridentata* in Sandy Soils of South Central Washington. Ph.D. Thesis, Washington State Univ., Pullman. 60 p.

Schlatterer, E. F., and E. W. Tisdale. 1970. Effects of litter of *Artemisia, Chrysothamnus* and *Tortula* on germination and growth of three perennial grasses. Ecol. 50: 869-873.

Received December 28, 1973.
Accepted for publication October 11, 1974.

R. Daubenmire

Department of Botany
Washington State University
Pullman, Washington

Plant Succession on Abandoned Fields, and Fire Influences, in a Steppe Area in Southeastern Washington

Abstract

In southeastern Washington, communities of mainly annual plants dominated by *Bromus tectorum* and *Chrysothamnus nauseosus* that had developed following the abandonment of cropland, or following overgrazing of natural steppe vegetation, have been compared with an essentially virgin stand dominated by *Agropyron spicatum* and *Poa sandbergii* which represents the pristine vegetation. The annuals quickly gain control and even after 52 years have largely resisted the reinvasion of the primary community, despite the availability of abundant seed—a situation strongly contrasted with the steppe area east of the Rockies. Competitive advantage for the annuals appears to rest on their relatively rapid rates of growth in winter and spring, resulting in their maturation before *Agropyron* seedlings have developed sufficiently to go into aestivation when the rainy season ends and the soil dries. Another native perennial bunchgrass, *Sporobolus cryptandrus,* is relatively successful in becoming established in the *Bromus tectorum* community and eventually becomes codominant with the *Bromus,* at least on land that has been repeatedly cultivated and abandoned.

Fire temporarily increased productivity in the two stands of the *Chrysothamnus-Bromus* community studied. In the *Agropyron-Poa* stand, production was reduced to 50 percent of normal in the first postburn season, with substantial recovery starting the next season. In neither community did fire have much of an influence on floristic composition other than to alter balances among the species. Burning normally kills *Chrysothamnus* back to the soil surface only, but a fire in July just after these shrubs had been defoliated by grasshoppers proved fatal to nearly every plant.

Lightly grazed steppe has deteriorated somewhat following the exclusion of cattle, suggesting that moderate grazing has a stimulating effect.

Immediately west of Clarkston, Washington, several smaller valleys extend southward from the main valley of the Snake River. The climate in the lower parts of these valleys is dry (median annual precipitation approximately 300 mm, falling mainly in winter, with mean July temperature rising above 20° C), and the soils are sandy. Those parts of the topography amenable to cultivation machinery have proven to be not very productive, and in consequence abandoned fields of varying ages are interspersed over land otherwise used for cattle grazing. The presettlement vegetation appears to have been mainly the *Agropyron spicatum-Poa sandbergii*[1] association (Daubenmire, 1970).

In one of the small valleys a remnant of essentially virgin vegetation that had been only lightly grazed was found adjacent to an old field that had been abandoned years ago and now supported a *Chrysothamnus nauseosus-Bromus tectorum* community. My interest in a comparative study of the old field and the natural vegetation beside it was shared by Mr. William Larson, owner of the property, who facilitated the investigation by fencing off an exclosure that included portions of both vegetation types. Results of this study through 1973 are reported here. Additional studies

[1] Plant names follow Hitchcock *et al.*, 1955-1969.

being made by Dr. Gary Benson on root growth of grasses and studies of the influence of weather on inflorescence production by *Agropyron* will be reported later. Since the vegetation on Mr. Larson's land is typical of a major type of steppe vegetation in Washington, none of which has been set aside as a natural preserve, it is hoped that the exclosure can be maintained indefinitely as an example of this type of vegetation in virgin condition, as an illustration of the fate of abandoned cropland, and as a site for other ecologic studies in the future.

The exclosure is located in S29 T11N R45E along a country road locally referred to as the Silcott Grade. The soil is classed as Farrell very fine sandy loam, a Regosol-Brown intergrade, and a Calcic Haploxeroll. The slope in the exclosure is approximately 16 percent to the NNW. The permanent transects used for a long-term trend studies are 25 m long and marked with steel stakes at either end. In the old field, 40 plots 20 x 50 cm in dimension were located at 0.5 m intervals on the north side of a line connecting the two stakes. In the virgin area a similar series of plots was located on the east side of the line. The canopy coverage method as described by Daubenmire (1959) was used for most analyses, and frequency is based on coverage. Basal area frequency refers to the percentage of 1,000 circular plots which included a living shoot at the ground surface. These plots were 40 mm in diameter and were distributed systematically.

The initial plan of study was to tally the same plots from time to time and, starting in 1959, to record any subsequent changes in vegetation composition; but in July, 1961, a fire ran across about half the *Agropyron-Poa* stand and most of the *Chrysothamnus-Bromus* stand. Accordingly, a new series of plots was established astride the burn lines to study burned and unburned areas comparatively. An appraisal of the results of the fire study after 12 years will be reported first.

Effects of Fire

Burning had relatively little impact on the *Agropyron-Poa* stand, except to change the balance among the species (Table 1). *Agropyron*, the outstanding dominant, was moderately reduced in coverage and frequency, but dry-matter production was reduced 50 percent in the first postburn season (Table 2). Basal area frequency was 7.7 percent in the unburned area and 8.1 percent in the burned area, showing clearly that fire did not reduce the basal area of the *Agropyron.* Since canopy coverage was reduced with no reduction in basal area, the tillers in the burned area were being held more stiffly erect. With lowered productivity, the tillers must also have been shortened by the fire. Judging from coverage and frequency data, the preburn status of *Agropyron* appears to have been restored by the twelfth year.

Poa prospered after the fire, undoubtedly as a consequence of the reduced spread of the taller *Agropyron* plants which allowed more insolation to reach the diminutive bunches of the *Poa.* The coverage of *Poa* more than doubled, and flowering increased tremendously (Table 1). On the fourth postburn year its basal frequency was 15 percent in the unburned area but still twice as high as normal (32 percent) in the burned. By the twelfth year this stimulation had essentially disappeared.

Among the minor species both *Achillea* and *Draba* were strongly reduced after the fire, whereas *Astragalus, Brodiaea, Erigeron, Festuca octoflora, Lithophragma,* and *Lomatium triternatum* were benefited. In the latter group, *Astragalus, Brodiaea,* and

TABLE 1. Effect of the 1961 fire on the *Agropyron-Poa* stand. Percentage canopy coverage to the left of the dot, frequency to the right.

Treatment	Unburned			Burned		
Postfire year	2nd	4th	12th	2nd	4th	12th
DWARF SHRUB						
Phlox longifolia	3.58	8.88	3.70	2.50	3.48	4.52
PERENNIAL GRASSES						
Agropyron spicatum	81.99	85.99	74.100	59.92	72.99	74.100
Poa sandbergii	10.88	13.100	2.72	25.98	36.98	7.88
PERENNIAL FORBS						
Achillea millefolium lanulosa	4.30	5.35	2.28	+.5	1.20	4.58
Astragalus inflexus	.	.	+.2	+.8	1.12	3.22
Brodiaea douglasii	+.2	.	+.5	1.32	1.48	1.22
Calochortus macrocarpus	1.30	1.25	1.42	.	1.28	1.35
Erigeron pumilus intermedius	1.18	1.15	+.2	2.65	+.2	+.2
Lithophragma bulbifera	.30	1.48	1.55	1.62	3.85	2.88
Lomatium macrocarpum	+.2	.	.	.	.	.
Lomatium triternatum	+.5	+.12	4.58	3.32	2.35	3.58
Tragopogon dubium	1.30	2.42	1.8	1.10	.	+.10
ANNUALS						
Bromus japonicus	1.42	1.30	1.32	+.10	+.5	+.18
Bromus mollis	4.80	1.45	.	.	.	.
Bromus tectorum	5.100	2.65	1.48	1.52	.	+.15
Draba verna	2.100	3.100	2.100	1.28	2.99	2.95
Epilobium paniculatum	.	+.20	+.5	.	+.20	.
Erodium circutarium	.	+.10	+.2	.	+.2	+.15
Festuca octoflora	.	1.28	1.30	2.85	1.62	+.2
Festuca pacifica	.	+.18	1.25	1.58	+.2	1.55
Holosteum umbellatum	6.99	9.99	10.100	3.93	6.99	17.100
Lactuca serriola	1.30	+.15	2.100	+.10	+.2	2.78
Montia perfoliata	.	.	1.38	.	.	+.8
Plantago patagonica	18.100	5.100	3.98	7.99	4.99	3.100
Stellaria nitens	+.5	1.28	2.85	+.5	+.8	1.58
Inflor./m^2 *Agropyron*	30	107	75	81	58	110
Poa	2	13	1	451	86	11

TABLE 2. Oven-dry weight of terminal standing crop of *Agropyron spicatum* shoots, with standard errors. Each value is the mean of four clipped plots, each 0.5 x 2.0 m. The species were clipped in sequences as they matured during spring and early summer.

Postfire year	Unburned (g/m^2)	Burned (g/m^2)
1st	118.3 ± 1.8	60.1 ± 4.2
2nd	74.9 ± 1.7	62.9 ± 1.8
3rd	146.2 ± 1.2	121.3 ± 1.6

Lithophragma appear to have been still a little overrepresented by the twelfth year. The annual species of *Bromus* were reduced by the fire and had not regained their former population levels by the twelfth postfire year. Other minor species vary so much from year to year that no clear fire influences were apparent.

In summary, the fire caused some minor changes in the *Agropyron-Poa* stand, but most of these were short-lived, and the previous balance among at least the leading dominants was restored by the twelfth postfire year.

In the *Chrysothamnus-Bromus* stand (Table 3) fire eliminated the *Chrysothamnus*,

TABLE 3. Effect of the 1961 fire on the *Chrysothamnus-Bromus* stand. Canopy coverage to the left of the dot, frequency to the right.

Treatment	Unburned			Burned		
Postfire year	1st	2nd	3rd	1st	2nd	3rd
MEDIUM SHRUB						
Chrysothamnus nauseosus	8.20	11.25	.*	.	.	.
PERENNIAL GRASS						
Poa sandbergii	1.8	.	+.5	1.20	1.12	1.10
PERENNIAL FORBS						
Achillea millefolium lanulosa	+.5	2.8	+.15	.	.	1.8
Astragalus inflexus	.	.	.	.	+.2	.
Lithophragma bulbifera	+.15	+.2	+.20	1.20	.	.
Lomatium macrocarpum	+.2	.	+.5	.	.	.
Tragopogon dubium	1.12	6.68	14.75	10.28	2.35	13.80
ANNUALS						
Bromus japonicus	.	.	.	.	.	+.2
Bromus mollis	.	.	.	.	.	+.2
Bromus tectorum	96.100	81.100	64.100	95.100	91.100	49.100
Draba verna	1.48	1.60	.*	+.5	.	.
Epilobium paniculatum	.	.	+.5	.	.	.
Erodium cicutarium	1.58	1.22	6.60	12.88	2.95	6.98
Festuca pacifica	1.28	+.10	.*	.	.	.
Galium aparine	.	+.2	.	.	.	.
Holosteum umbellatum	47.98	23.100	21.00	6.85	18.100	39.100
Lactuca serriola	.*	2.82	1.40	+.8	1.42	1.50
Plantago patagonica	2.38	2.48	1.32	1.15	3.58	1.25
Sisymbrium altissimum	2.35	+.2	1.45	1.18	+.2	+.20
Stellaria nitens	.	+.2	1.25	.	.	.

*Not recorded.

but under unusual circumstances, which will be detailed later. Ordinarily, following steppe fires, this shrub sprouts readily from adventitious buds at the summit of the root.

Poa sandbergii again appeared to benefit slightly from the fire. The soil remained denuded of its normal dense cover of standing *Bromus* litter from July, the time of the fire, until the following spring. The perennial *Poa,* regenerating tillers from undamaged underground parts, exploited the strong insolation while the *Bromus* was germinating and developing slowly in fall and winter, then managed to retain its improved status for at least two years.

Draba, Holosteum, and *Festuca pacifica* were reduced in amounts in at least the first postfire season, while *Erodium* was greatly benefited. *Erodium* is more responsive to heat than is *Bromus tectorum* (Table 4), and this probably accounts for its general increase immediately following steppe fires.

In a plot 20 x 50 cm located in a representative part of the unburned fragment of the *Chrysothamnus-Bromus* community, 918 plants of *Bromus* spp. were counted, and the oven-dry weight of their shoots clipped at the soil surface just prior to dissemination was 14.35 gm. Calculated to a square-meter basis, this amounts to 9,180 plants weighing 143.5 gm. In a representative 1 x 1 m plot on the burned side of the ecotone there were only 327 plants, having a combined weight of 187.6 gm. Thus, on the burned area there appeared to be only 1/28th the population density, but each plant had more than 30 x the dry weight. In the second postfire season there was no evident difference between burned and unburned areas, except for the absence of living *Chrysothamnus.*

The summer of the fire was one of those occasional years when grasshoppers

TABLE 4. Percent germination based on total seeds out of a lot of 50 which germinated either during the test period or afterward, when the germination chambers were removed to a warm room.

Species	Temperature range in °C	Cumulative germination at end of: 24 hrs.	48 hrs.	72 hrs.	96 hrs.	120 hrs.	144 hrs.
Bromus tectorum	0- 2.5	0	0	0	0	0	0
	3- 5	0	0	0	0	0	3
	7-11	0	0	0	25	63	68
	10-13	0	0	21	82	87	87
	22-24	40	100	100	100	100	100
Erodium cicutarium	0- 2.5	0	0	0	0	30	71
	3- 5	0	0	46	86	98	98
	7-11	0	59	90	93	95	95
	10-13	7	95	98	98	98	98
	22-24	84	98	100	100	100	100

are overly abundant, and as usual when the *Agropyron* leaves began to dry in late June, these insects turned to the foliage of *Chrysothamnus*, the only species with much phytomass which normally remains green all summer. By the time of the fire in July the *Chrysothamnus* bushes had been stripped of their leaves. Usually fire does no more than to kill this plant back to the soil surface, and it sprouts immediately from the summit of the tap root. However, it soon became apparent that in this fire the shrub population had suffered heavy mortality.

In the second postfire season ten parallel lines, each 25 m long, were established on either side of the burn line in the *Chrysothamnus-Bromus* community, and the living and dead plants crossed by these lines were counted. The data revealed approximately 97 percent mortality (Table 5). Dead plants that had died previous

TABLE 5. Numbers of dead and living (any part) bushes of *Chrysothamnus nauseosus* bushes crossed by lines established in adjacent burned and unburned parts of the *Chrysothamnus-Bromus* community in 1963, two years after the fire.

25 m lines	Burned dead	Burned alive	Unburned dead	Unburned alive
I	5	1	4	5
II	6		2	11
III	8		7	4
IV	7		9	5
V	8	1	9	5
VI	8		9	4
VII	5		4	8
VIII	5		2	7
IX	6		7	10
X	10		3	8
Totals	68	2	56	67

to the fire, due to unknown causes, were thoroughly dry and so were entirely consumed by the fire. The dead plants tallied in the burned area represented those that were alive at the time of the fire and so were scorched and killed but not wholly consumed. Thus, just the live plants in the unburned area are equivalent to the dead plus live plants recorded in the burned area.

The circumstance described above suggests that an effective way of eliminating *Chrysothamnus* from rangeland where it has increased due to misuse might be to

burn the vegetation following defoliation by grasshoppers or perhaps by chemicals. Neither fire alone, nor grasshopper defoliation alone, has a drastic effect on this shrub.

Natural Revegetation of Abandoned Fields

The special series of plots established to determine fire influence indicated that except for *Chrysothamnus* the prefire equilibrium was essentially re-established by the twelfth postfire year; therefore, the original series of plots established for the study of long-term trends was considered usable without regard to the fact that fire had run over a large share of them.

That portion of the exclosure which has once been cultivated is a slender extension of an old field that had to be abandoned when it was cut off from the remainder of the field by a road extended up the valley. It has been fairly well established that this took place in 1920. Accordingly, the abandoned field was 39 years old when I began to record its composition.

Immediately to the west across the road is the remainder of the same field, that continued to be cultivated intermittently until 1958, and upon its abandonment at that time I commenced a study of that area too in the following summer. Since topography and soil are quite comparable on both sides of the road, it seems reasonable to link the first 12 years of vegetation change recorded in the younger field with studies in the exclosure which represented 39 to 52 years, using the virgin area as an indication of the presettlement vegetation and possibly of the climax toward which both fields are advancing. This has been done in Table 6.

TABLE 6. Composition of vegetation in three contiguous stands representing a time sequence. Percentage canopy coverage to the left of the dot, frequency to the right.

Stand	Younger Field						Older Field				Virgin	
Years since abandonment	1	2	3	4	5	12	39	40	41	52	1959	1972
MEDIUM SHRUBS												
Chrysothamnus nauseosus	+	+	+	+	+	+.2	20.48	24.48	24.48	1.8	1.5	+.2
DWARF SHRUB												
Phlox longifolia	.	.	.	.	.	.	.	.	.	.	2.50	3.68
PERENNIAL GRASSES												
*Agropyron desertorum***	2.18	4.25	1.8	1.2	1.2	5.8	.	.	.	.	.	.
Agropyron spicatum	.	.	.	.	.	.	+.5	1.5	.	.	86.99	78.99
Poa sandbergii	.	.	.	.	.	.	3.15	+.5	.	+.2	39.99	5.75
Sitanion hystrix	.	.	.	.	.	.	+.5	+.10	+.2	+	.	.
Sporobolus cryptandrus	.	.	.	.	.	6.15	.	.	.	2.5	.	.
PERENNIAL FORBS												
Achillea millefolium lanulosa	+	+	+.12	.	+.2	+.5	1.5	4.15	2.15	+.5	1.20	7.62
Agroseris grandiflora	.	.	.	.	.	.	.	.	.	–	.	.
Astragalus inflexus	+	+	+.2	.	+.2	.	+	.	+.2	.	+	5.18
Brodiaea douglasii	.	.	.	.	.	+	+.2	+.2	.	+.5	+	1.35
Calochortus macrocarpus	.	.	.	.	.	.	+.2	.	.	.	.	1.38
Crepis acuminata	.	.	.	.	.	.	+	.	.	.	.	.
Erigeron pumilus	+	+	.	.	–	.	+	.	.	.	+.12	+.2
Lithophragma bulbifera	.	.	.	.	.	.	.	+.5	.	1.18	2.45	4.82
Lithophragma parviflora	.	.	.	.	.	.	+	.	.	+.2	.	.

TABLE 6. (continued)

Stand	Younger Field						Older Field				Virgin	
Years since abandonment	1	2	3	4	5	12	39	40	41	52	1959	1972
Lomatium macrocarpum	.	.	.	.	.	.	.	.	.	+.5	.	.
Lomatium triternatum	.	.	.	.	.	.	+	.	.	.	+.2	2.62
*Medicago sativa***	1.5	4.28	1.20	.	.	.	.	.	.	.	.	.
Microseris troximoides	.	.	.	.	.	.		.	.	.	.	+.15
Sphaeralcea munroana	+	.	.	.	.	.	+	.	.	.	.	1.2
ANNUALS AND BIENNIALS												
Amsinckia intermedia	.	.	.	+.2	.	.	.	.	.	.	.	.
**Bromus japonicus*	+.5	+.2	+.8	1.25	1.40	3.78	1.18	+.2	.	.	+.5	+.15
**Bromus mollis*	+.10	+.5	+.10	1.22	1.20	1.55	1.30	1.28	3.42	+.12	1.25	.
**Bromus tectorum*	8.99	57.99	24.99	26.99	36.99	14.99	61.99	—	74.99	7.99	+.20	+.18
Cirsium undulatum	.	.	.	.	.	.	.	.	.	1.2	.	.
Conyza canadensis	.	3.58	.	.	1.42	.	.	.	.	.	.	.
**Draba verna*	.	+.2	1.55	+.18	1.35	7.99	3.98	2.65	2.95	3.99	6.99	4.99
Epilobium paniculatum	+.5	4.98	2.90	+.5	+.22	1.28	2.52	2.85	+.12	+.5	+.12	+.18
**Erodium cicutarium*	+.12	5.92	32.99	41.99	38.99	48.99	4.98	3.99	12.98	1.32	+.18	+.5
Euphorbia glyptosperma	.	+.2	.	.	.	2.85	.	.	2.62	.	.	.
Festuca octoflora	.	.	+.2	.	.	.	.	+.2	.	.	2.82	.
Festuca pacifica	+.8	.	+.2	.	.	1.28	3.50	1.28	2.70	+.20	1.38	1.35
Gallium aparine	.	.	.	.	.	.	+	.	.	.	.	.
Helianthus annuus	+	3.32	+	–	29.98	8.48	+	+	+	+	.	.
**Holosteum umbellatum*	+.2	+.8	4.98	16.99	22.99	11.99	5.99	2.93	8.99	14.99	9.99	6.99
**Lactuca serriola*	+.5	2.50	6.75	+.10	+.5	+.5	+.18	1.45	—	24.99	+.15	3.80
Lagophylla ramosissima	+.2	+.2	.	.	+.2	.	+.5	+.5	.	.	.	.
Lepidium densiflorum	+.5	.	.	.	.	.	.	.	.	.	.	.
**Lepidium perfoliatum*	+	.	.	.	+.2	.	.	+.2	+.2	+.2	.	.
**Melilotus officinalis*	.	.	.	.	.	+.5	.	.	.	+	.	.
Montia perfoliata	.	.	.	.	.	.	.	.	.	+.5	.	1.32
Plantago patagonica	2.62	8.65	7.88	7.99	7.99	1.38	1.32	—	1.40	1.55	3.99	4.99
**Salsola kali*	.	.	.	.	1.5	.	.	.	.	+.2	.	.
**Sisymbrium altissimum*	+	4.45	2.48	2.68	1.25	.	+.2	+.5	.	+.2	.	.
Stellaria nitens	.	+.2	1.38	1.22	+.15	1.25	1.25	+.10	1.40	+.2	2.90	1.35
**Tragopogon dubius*	+	3.35	2.32	3.25	3.40	.	+.12	7.40	2.35	1.2	+	1.12
Σ coverages, excl. *Chrysoth.*	13	97	83	99								
% coverage by annuals	77	89	95	96	142 97	109 90	86 95	— —	109 96	65 92	154 16	125 16

*Alien species, adventive.
**Alien species, planted.

As the last crop was harvested from the young field, *Agropyron desertorum* and *Medicago sativa* were planted, but since cattle had access to the area, and little desirable forage was available most of the year, the latter plant was quickly eliminated, and the former did not contribute much phytomass.

The most striking feature of the data is the manner in which *Bromus tectorum* gained control by the second postfire season and has maintained control in the older field for 52 years! *Erodium* entered the young field more slowly than *Bromus*, and from the third through the twelfth year its coverage exceeded that of the *Bromus,* owing to its rosette form in contrast with the erect form of *Bromus.* Records from the older field show that the vigor of *Erodium* eventually declines.

Other alien annuals, chiefly *Bromus japonicus, B. mollis, Holosteum umbellatum,* and *Lactuca serriola*, make a substantial contribution to the old field vegetation, although collectively they are inferior to *Bromus tectorum* and *Erodium* in most years. *Chrysothamnus* slowly gains ground, eventually becoming much more important in the disturbed than in the virgin community. Typically, coverage of *Chrysothamnus* amounts to 20-30 percent when more extensive sampling is done in the *Chrysothamnus-Bromus* stands in eastern Washington, where it commonly takes over after either cultivation or excessive grazing has eliminated any of several types of primary vegetation.

Sporobolus cryptandrus will clearly dominate the young field if present trends are not interrupted, for west of the road, in adjoining fields of less recent abandonment, it has achieved this status. However, in the older field within the Larson exclosure east of the road, there were only 13 plants of *Sporobolus* in 1974. In this old field there are 133 plants of *Agropyron* scattered over the formerly plowed land. These include individuals of all sizes producing an abundance of caryopses annually, yet young plants obviously have difficulty in becoming established in the surrounding matrix of *Bromus tectorum. Agropyron* and *Bromus* both germinate in autumn and grow slowly all winter, but *Bromus* develops rapidly and matures its caryopses by the time soil moisture approaches exhaustion in early summer, whereas by this time the seedling perennial has not developed sufficiently to aestivate. *Agropyron* can be sufficiently developed to endure desiccation by late June only where competition is negligible (Daubenmire, 1968). Harris (1967) has shown that *Bromus tectorum* extends its root system rather continuously at low temperatures, whereas the growth of *Agropyron* roots practically ceases in cold soil. Hulbert (1955) found that *Bromus tectorum* in this habitat type may extend its roots to a depth exceeding 120 cm. The similarity in rooting depth of the two grasses, combined with differences in winter root growth and degree of development at the time of moisture exhaustion, can easily account for the rather regular elimination of *Agropyron* seedlings by *Bromus.* The only other perennial grass in this area in 1974 was *Sitanion hystix* represented by 60 individuals.

The cultivated area in the exclosure had been cropped probably only once or just for a few seasons, and the scattering of plants there now may represent the progeny of *Agropyron* seeds that survived cultivation and then became established prior to the immigration of *Bromus tectorum.* It is not known when *Bromus* arrived in this valley, but it is significant that no annual bromes were mentioned in Weaver's (1917) monograph on the vegetation of southeastern Washington.

Sporobolus is a common perennial bunchgrass in the lower parts of the valleys of the region as a whole. Although there is some evidence of its climax status on certain soils (Daubenmire, 1970), it is certainly seral in the vicinity of the Larson exclosure. On old fields west of the road that appear to have been alternatively cultivated and abandoned for decades, *Sporobolus* appears and increases progressively after each abandonment. It does this despite a heavy *Bromus* cover, but the *Bromus* persists as a lower grass layer. Long-lived seeds of *Sporobolus* probably persist during cropping or are carried into the fields on the feet of cattle to provide the start of a new stand. *Agropyron* seeds, in contrast, appear to live but a short time, and the seedlings are far less successful than *Sporobolus* in competition with *Bromus*.

It is always possible that factors other than competition may exclude a plant such as *Agropyron* from entering the established community dominated by *Bromus*, so that some attention was given to the possibility that vitality, allelopathy, or caryopsis predation by animals might be involved.

Caryopses from the old *Agropyron* plants located in the *Bromus* community proved highly fertile. They grew equally well in a glasshouse when planted in the upper 5 cm of soil obtained from both *Chrysothamnus-Bromus* and *Agropyron-Poa* stands. Thus, vitality is unimpaired, and there would seem to be no allelopathy involved here.

If rodent or bird uses of the two communities differed, predation might account for the seedlings' failure to appear where *Bromus* dominates. Sets of 100 caryopses were inserted vertically in the soil at 1 cm intervals in a line. One such set was completely screened with 0.5-inch mesh hardware cloth, with another set, under the same type of screen but elevated 2 cm to give easy access to mice. Similar pairs of plantings were made in both communities, and the resulting seedlings were counted from time to time. The results were essentially identical for all sets. Seedlings appeared abundantly in autumn, grew slowly with little mortality during winter, but in late spring as the soil began to dry, the single weak tillers, seldom 8 cm tall, invariably succumbed. Predation by mice appeared to be zero. Caryopses inserted vertically in the soil to a distance equal to their length could well have a measure of immunity to discovery; however, natural cracks resulting from drying or frost action occur abundantly, yet they sponsor no successful seedlings. Bird predation is, therefore, not likely to be responsible for the complete failure of tens of thousands of seeds produced nearly every year.

Intense competition in both closed communities appears to be fatal to *Agropyron* seedlings. The alien annuals germinate no earlier but have the advantage of rapid development to maturity. That they are competitively superior to *Agropyron* seedlings even in the *Agropyron-Poa* community is demonstrated by the thin populations of *Bromus* spp., *Draba, Holosteum, Erodium,* etc., that can maintain themselves year after year in the virgin stand, whereas young plants of *Agropyron* regularly fail.

Poa sandbergii, the second most important species in the virgin vegetation, is only slightly better able to meet competition. It has the advantage of completing its vegetative and sexual activities during winter and spring, then going into aestivation while *Agropyron* and the *Bromus* species are still actively growing. Its disadvantage is short stature combined with high insolation requirements. Although *Poa* is a perennial, it is short-lived, so that the populations are in a constant state of flux, which is reflected in the data.

Chrysothamnus also appears short-lived for a woody plant, as witnessed by the appreciable numbers of dead bushes tallied in the unburned part of the old field (Table 6) and by the high variability in its coverage in the permanent plots in the old field. The decrease of this plant in the virgin area between 1959 and 1972 reflects mortality in that half of the stand which was burned. This shrub is regularly present in very small amounts in virgin stands of the *Agropyron-Poa* association over a wide area in eastern Washington (Daubenmire, 1970).

It may be observed (Table 6) that there has been a deterioration of the vegetation in the *Agropyron-Poa* stand between 1959 and 1973. Summed coverages of all species, exclusive of *Chrysothamnus*, have declined from 154 to 125. Considering just the two perennial grasses, the corresponding sums are 125 and 83. Much of this strong reduction in perennial grass coverage has been compensated by an increase in forb coverage, for there has been negligible change among the annuals.

This deterioration cannot be attributed to the few rabbits present, for evidence of their use of the herbage is seldom seen. Neither has there been any notable change in weather. A likely explanation is that light grazing prior to the erection of the exclosure and start of study had kept the grasses stimulated, and since forbs are more readily damaged by defoliation and trampling, they consequently increased under protection.

If we may assume that the sums of coverages are somewhat proportional to the degree to which foliage is intercepting light, then there was a deficiency of foliage in only the first year after field abandonment. For the next half century there was wide fluctuation with no unidirectional trend, and coverage equaled that in the virgin area in relatively moist years. The labile character of the *Chrysothamnus-Bromus* community is well illustrated by *Lactuca* which covered 24 percent of the area in 1972 but was difficult to find in 1974.

Despite the abortive attempt to establish *Agropyron desertorum* and *Medico* when the young field was abandoned, annuals plus the biennial *Tragopogon* gained complete control of the abandoned field the first year and evidently can retain control for at least half a century.

The young *Agropyron spicatum* plant encountered in the *Bromus* stand in the exclosure in years 1939 and 1941 had succumbed by the time of the 52-year tally. *Poa sandbergii,* a short-lived opportunist, apparently encounters difficulty in the *Bromus* community despite the relatively short stature of the annuals.

The situation at the Larson exclosure is distinctly different from the steppe region east of the Rockies, where in 50 to 100 years a community approximating the pristine condition can become re-established naturally (Booth, 1941; Costello, 1944; Kucera and Aikman, 1951). This tenacity of aliens to maintain themselves indefinitely, once established on disturbed land, seems to characterize all the steppe vegetation of eastern Washington.

Snake River Canyon Study

Observations at the Larson exclosure can be supplemented with the results of studies of fire influences in another *Chrysothamnus-Bromus* stand in the *Agropyron-Poa sandbergii* habitat type located on the scarp directly north of Lewiston, Idaho. This site had been grazed excessively for many years but never cultivated. Although the fire

had passed over part of the stand rapidly and had hardly blackened the soil surface, it was hot enough to kill all aerial parts of the *Chrysothamnus* plants. Frequency analyses in the spring following the August fire provided a fairly complete list of the flora and showed that, although there are some increases and decreases in representation, the fire in general had little influence on species' frequencies (Table 7).

TABLE 7. Rooted frequency as measured by 100 plots each 2 x 5 dm, spaced at 1-m intervals along either side of a burn line.

Treatment	Unburned	Burned
DWARF SHRUB		
Phlox longifolia	3	0
PERENNIAL GRASSES		
Poa sandbergii	42	49
Sitanion hystrix	19	9
PERENNIAL FORBS		
Achillea millefolium lanulosum	49	68
Allium acuminatum	1	0
Brodiaea douglasii	67	50
Fritillaria pudica	4	5
Gaillardia aristata	29	7
Lithophragma bulbifera	83	90
Lithophragma parviflora	23	21
Lithospermum ruderale	0	1
Lupinus leucophyllus	67	14
Lupinus sericeus	9	34
ANNUALS AND BIENNIALS		
Amsinckia intermedia	59	56
Bromus mollis	21	18
Bromus tectorum	100	100
Cerastium viscosum	0	2
Cirsium undulatum	0	2
Collomia linearis	2	4
Draba verna	97	99
Epilobium paniculatum	5	5
Erodium cicutarium	78	96
Festuca pacifica	95	95
Lactuca serriola	97	21
Lappula redowskii	0	2
Madia exigua	8	2
Microsteris gracile	9	23
Montia parviflora	56	18
Sisymbrium altissimum	27	58
Stellaria nitens	100	97
Veronica arvensis	92	36

Helianthus annuus, which develops late and was not included in the spring tally, was evidently less abundant in the burned[2] area.

Five representative plots, each 2 x 10 dm, were clipped on either side of the burn line on April 30 and May 28, and only those species were harvested that were estimated to have achieved full shoot growth on each date. The results (Table 8) show that in the burned area *Bromus tectorum* produced relatively large plants, resulting in increased dry matter per unit area in the first postburn season, as compared with the control. Most of the minor species had little phytomass and were ignored, but

[2] Fires sweep the area from time to time, as they do all of this scarp, but the "unburned" area had not been burned in recent years.

TABLE 8. Oven-dry weight of shoots of principal species in the first postburn season, at approximately the time each attains maximum development.

Species	g/m^2 Unburned	Burned
Bromus tectorum	100.20	128.75
Sitanion hystrix	6.10	+
Lupinus leucophyllus	4.11	.30
Lupinus sericeus	1.80	1.00
Sisymbrium altissimum	1.75	3.35*
Poa sandbergii	1.12	5.60*
Erodium cicutarium	.52	14.20
Amsinckia intermedia	.40	2.56
Totals	116.00	155.76

*These plants were grazed before the clipping was done, so that the figures do not represent total production.

of those that seemed worthy of study, *Sitanion* and the two species of *Lupinus* were adversely affected by the fire, whereas four other species were considerably benefited. *Erodium cicutarium* was outstanding in the latter group. Although the frequency of this species was increased about only 25 percent by the fire, the individuals on the burned area were so much larger that its productivity was 28 x greater.

A study was made of the numbers of seeds and their distribution in the unburned area by collecting layers of soil in a plot 2 x 10 dm, in August when the seed cast was complete. The 0 to 5-, 5 to 10-, and 10 to 15-mm horizons were sampled separately and stored dry in the laboratory until mid-winter. Then each collection was thoroughly mixed, and a weighed portion spread over a layer of moist sterile sand in a covered glass dish. As the seedlings appeared, they were removed with forceps and counted. After germination had apparently ceased, the dishes were uncovered, allowing the soil to become air-dry, then the soil was moistened once more, with the result that another crop of seedlings was obtained. This treatment was repeated three times, and finally the moistened material was subjected to a temperature of 0 to 2° C for two months to obtain still more germination.

Except for *Lithophragma bulbifera*, none of the species recognized seemed to require a cold treatment to break dormancy. All seeds of *Bromus, Festuca,* and *Erodium* which germinated appeared promptly following the first moistening of the soil.

The results (Table 9) show that in the upper 15 mm of the soil there were approximately six seeds per square centimeter of soil surface. By far the bulk of

TABLE 9. Number of seeds per square meter of soil surface, as determined by laboratory germination tests.

Soil Horizons in mm	*Bromus** spp.	*Festuca pacifica*	*Erodium cicutarium*	Other dicots	Totals
0- 5	9,657	20,213	315	14,523	
5-10	1,122	2,397	289	2,285	
10-15	198	540	198	6,804	
Totals	10,977	23,150	802	23,612	58,541

*Mainly *B. tectorum*, but this species and *B. mollis* cannot be distinguished in the early vegetative stages.

the seeds in this community of annuals is contained in the very surface layer. Heady's (1958) count of 35 seedlings per square inch (= 5.3/cm^2) in comparable annual-dominated grassland in California is remarkably similar to the results obtained here.

Since *Bromus* produced only 13 x as many seeds per unit ground surface as *Erodium,* while its productivity was 200 x greater, there must be a normal advantage to *Bromus* in competition that is reversed by burning. The differential response of the seeds to the presumably warmer soil in the burned area is probably important as pointed out earlier. Also, deeper storage of *Erodium* seeds as a result of the action of their hygroscopic awn may have resulted in less mortality during the fire.

Owing to intensive grazing over a large area in which this study was conducted, there is no seed source for either *Agropyron* or *Sporobolus.*

Literature Cited

Booth, W. E. 1941. Revegetation of abandoned fields in Kansas and Oklahoma. Am. J. Bot. 28: 415-422.

Costello, D. F. 1944. Natural revegetation of abandoned plowed land in the mixed prairie association of northeastern Colorado. Ecology 25: 312-326.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33: 43-64.

———. 1968. Soil moisture in relation to vegetation distribution in the mountains of northern Idaho. Ecology 49: 431-438.

———. 1970. Steppe Vegetation of Washington. Wash. Agric. Exp. Sta. Tech. Bull. 62, 131 pp.

Harris, G. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum.* Ecol. Mono. 37: 89-111.

Heady, H. F. 1958. Vegetational changes in the California annual type. Ecology 39: 402-416.

Hitchcock, C. L., *et al.* 1955-1969. Vascular Plants of the Pacific Northwest. Parts 1 to 5. Univ. of Washington Press.

Hulbert, C. L. 1955. Ecological studies of *Bromus tectorum* and other annual bromegrasses. Ecol. Mono. 25: 181-213.

Kucera, C. L., and J. M. Aikman. 1951. Secondary plant succession on an eroded Lindley soil as affected by variations in cultural treatment. Iowa State Coll. J. Sci. 25: 581-597.

Weaver, J. E. 1917. A study of the vegetation of southeastern Washington and adjacent Idaho. Univ. Nebr. Studies 17: 1-133.

Received July 9, 1974.
Accepted for publication August 22, 1974.

Grant A. Harris
Dept. For. & Range Mgt.
Washington State Univ.
Pullman, WA 99163

Northwest Science

Ronald J. Taylor
Department of Biology

and

Theodore R. Boss
Department of Geography
Western Washington State College
Bellingham, Washington

Biosystematics of Quercus garryana in Relation to its Distribution in the State of Washington

Abstract

Chemical (phenolic) and morphological parameters of 99 specimens of *Quercus garryana* (Garry oak) were systematically sampled, representing the geographical distribution of that species in the state of Washington. Based on paper chromatographic profiles of phenolic compounds, indices of similarity were determined for all combinations of specimens and the plants were grouped accordingly. The nature of variation (intraspecific versus intrapopulational and intra-individual) is implicit in the pattern of grouping and its significance is discussed. The results of this study showed only minor morphological or phenolic distinction among isolated populations and little correlation between the pattern of similarities and geographical distribution. The possible origins of oak populations in Washington are discussed.

Quercus garryana (Garry oak) is a member of the subgenus *Lepidobalanus* (white oaks) and like other North American oaks is derived from the Madro-tertiary Geoflora (Axelrod, 1958). Its present range is from south-central California to southern British Columbia, occurring in dense, pure stands, open savanna-like communities, or mixed forests. It occurs within the 25-40-inch rainfall zone, although the most important factor in delimiting its distribution is the small amount of rainfall (4-10 inches) received during the April-September growing season (USDA, 1965). With greater summer precipitation, *Quercus garryana* is replaced by faster growing, more competitive coniferous species such as *Pseudotsuga menziesii* (Sprague and Hansen, 1946). Garry oak is most frequently found on gravelly, well-drained slopes but occasionally occurs on deep loams or heavy clays in river valleys (Thilenius, 1968). Although *Quercus* species are notoriously highly specific in their edaphic requirements (Muller, 1952), the ecological success in Washington of Garry oak depends in large part upon this tree's rather broad edaphic tolerance and ability to grow on "poor" sites.

Garry oak is a member of an interbreeding complex (the *Lepidobalanus* syngameon) including such unlikely representatives as evergreen shrubs and deciduous trees (Grant, 1971; Tucker, 1953; and Tucker, personal communication, 1973). Within this syngameon, Garry oak appears to occupy a cytologically intermediate position—although its hybrids normally produce abortive acorns (Tucker, 1953)—and is probably the most variable member.

In spite of the fact that Garry oak has been intensively investigated in connection with the *Lepidobalanus* syngameon, little work has been done concerning its intraspecific relationships, and the pattern of variability has not previously been sampled in Washington. In the present study, an attempt has been made to correlate distribution with chemical and morphological parameters, through the patterns of similarity of these parameters, and, if possible, to trace migratory routes.

Materials and Methods

Oak-leaf specimens were systematically collected on a state-wide basis in July and August, 1973, and again in October, 1973 (see Fig. 1 and Table 1). This enabled an analysis of intraspecific and intrapopulational variation over time and space. Intrapopulational variation was tested by sampling 20 specimens in each of three large, well-separated populations (Table 1); and intra-individual variation—seasonal variation within individuals—was observed in several plants sampled on both collecting dates. Collections were made at approximately 6-7 ft above the ground, if possible, and included leaves from all exposures. It was not possible to restrict sampling to uniform-sized trees. During the October collection, leaves were selected in all states of senescence in order to test the aging effect on phenolic compound distribution. This effect proved to be negligible on a presence or absence basis for phenolics except in the case of anthocyanin which accumulates in senescent leaves.

The leaves were examined morphologically and chemically. Morphological characteristics included various size measurements, the pattern of lobing, and the nature and extent of pubescence. These parameters showed no recognizable pattern of variation except that resulting from adverse growth conditions. For the chemical analysis, leaf phenolics were extracted in methanol (MeOH) from 3-gm samples of dried

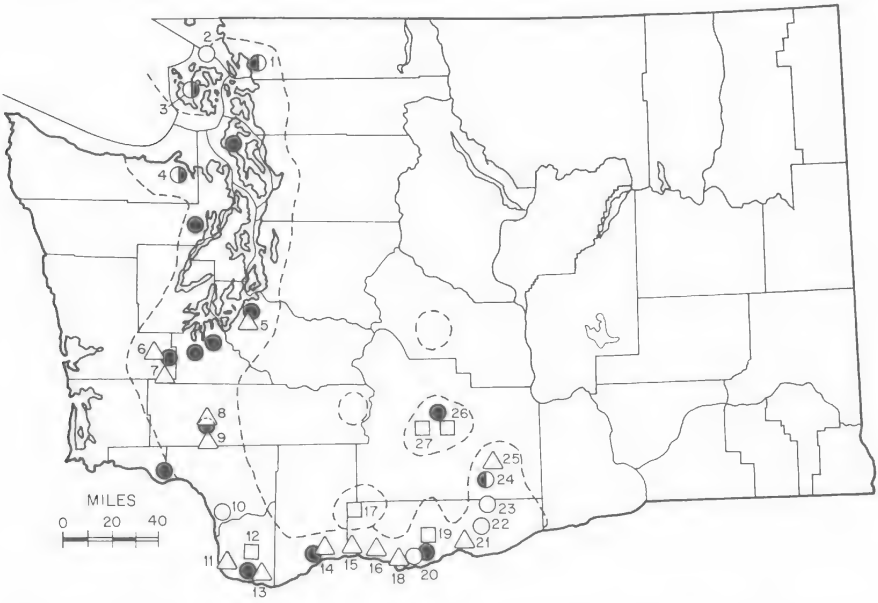


Figure 1. Collection sites and range of *Quercus garryana* and known geographical distribution of Indian villages. The open circles represent collection sites of October, 1973; the squares represent sites of July and August, 1973; and the triangles represent sites of both July and August, and October. The closed circles represent sites of previous Indian villages (after Swarton, 1968). The half-open, half-closed circles indicate complete overlap between October collecting-sites and villages. The dashed lines show the distributional range of Garry oak in Washington (with reference to USDA, 1965). The numbers relate to those in Table 1 where additional collection information is given. See Table 3 for additional information concerning Indian villages.

TABLE 1. Time and location of collections.

Number[2]	Location[1] County	Site	Time of Collection (1973)
1	Whatcom	South Bellingham	August
2	San Juan	Sucia Island	October
3	San Juan	San Juan Island	October
4	Clallam	Sequim	October
5	Pierce	McChord-Lakewood Exit, I-5	July, October
6	Grays Harbor	Oakridge	July, October
7	Grays Harbor	Oakville[3]	July, October
8	Lewis	Onalaska Exit, I-5	July, October
9	Lewis	Winlock Exit, I-5	July, October
10	Cowlitz	Woodland	October
11	Clark	NE 194 & NE 10 Vancouver	August, October
12	Clark	Hockinson	August
13	Clark	Washougal River[3]	August, October
14	Skamania	Hamilton Creek	August, October
15	Skamania	Cooks	August, October
16	Klickitat	Bingen	August, October
17	Klickitat	Trout Lake	August
18	Klickitat	Lyle	August
19	Klickitat	Blockhouse	August
20	Klickitat	Wishram Heights	October
21	Klickitat	Goldendale	August
22	Klickitat	South Satus Pass	October
23	Klickitat	Summit, Satus Pass	October
24	Yakima	8 mi north Satus Pass[3]	October
25	Yakima	12 mi north Satus Pass	August, October
26	Yakima	Confluence Naches & Tieton R.	August
27	Yakima	Troutlodge	August
28		Corvallis, Oregon[4]	October

[1] See Figure 1 for a state-wide distributional pattern.
[2] The collection numbers correspond to those of Figure 1.
[3] Large populations from which 20 specimens were collected.
[4] Not shown on the map of Figure 1.

leaf material for a period of 72 hours at 4°C. Two-dimensional paper chromatograms were developed from these extracts after they had been filtered and evaporated to dryness and their residue had been redissolved in 6 ml of MeOH (2 ml/gm dry weight of the leaves). Two chromatograms were developed for each specimen, one chromatogram spotted with 0.1 ml of extract, and the other with 0.25 ml of extract. The first developing solvent was tertiary-butyl alcohol: acetic acid: water, 3:1:1 (v/v/v), and the second was 15 percent acetic acid. The resulting phenolic spots were characterized using ultraviolet light, with and without the standard test reagents, ammonia and 2 percent aluminum chloride in ethanol, and by Rf values (Table 2). No positive identification of the phenolic compounds was attempted.

At the time specimens were collected for character analysis, observations concerning associated vegetation were made and recorded. These observations were descriptive in nature and did not involve quantitative sample analyses.

Results

Morphological variation was not as great as expected, and in many cases the entire range of variation could be observed in single specimens (excepting those associated with abnormal development in adverse habitats). In any case, the only recognizable pattern of morphological variation appeared to be environmentally induced.

In the chemical analysis, a total of 60 phenolic compounds were observed and

TABLE 2. Phenolic properties[1] and occurrence.

Compound No.	Rf values X 100 TBA/HAc[2]	UV	UV + NH_3	UV + $AlCl_3$	Frequency of Occurrence[3]
		Major Pigments			
1	50/42	Ab	b. Y	b. YFl	1.0000
2	36/31	Ab	Y-O	b. YFl	1.0000
3	65/30	Ab	G	b. YFl	1.0000
4	51/3	Ab	Y-G	b. YFl	1.0000
5	55/1	Y-OFl	brighter	b. GFl	1.0000
6	23/25	p. BFl	p. Y	B-WFl	1.0000
7	53/79	GFl	no change	no change	1.0000
8	46/86	b. BFl	no change	no change	1.0000
9	83/70	p. BFl	little change	no change	1.0000
10	72/58	p. BFl	little change	no change	1.0000
11	8/62	Ab	b. YFl	no change	1.0000
12	39/10	p. YFl	no change	Y-GFl	1.0000
13	74/1	p. Y-OFl	little change	no change	1.0000
14	89/15	Ab	no change	v. p. YFl	1.0000
15	81/47	w. Ab	w. Y	YFl	0.9286
16	46/63	v. p. PFl	no change	no change	0.9959
17	13/20	p. YFl	no change	p. Y-OFl	0.9796
18	16/13	p.YFl	no change	p. Y-OFl	0.9592
19	22/47	p. BFl	little change	no change	0.9184
20	64/60	p. W-GFl	no change	no change	0.8653
21	76/85	-	b. BFl	no change	0.8571
22	27/73	-	p. BFl	no change	0.8347
23	78/63	BFl	disappearing	disappearing	0.9490
24	55/64	Ab-Gray	Ab-Gray	no change	0.8102
25	33/72	-	-	YFl	0.7857
26	63/48	-	-	p. BFl	0.8408
27	83/80	-	Y-GFl	no change	0.8510
28	40/20	WFl	no change	no change	0.7857
29	91/71	-	p. BFl	no change	0.7857
30	19/88	GFl	no change	fades out	0.3367
		Minor Pigments			
31	28/20	p. YFl	no change	no change	0.6837
32	35/2	p. YFl	Y-O	l. GFl	0.3061
33	27/64	p. Y-GFl	no change	p. YFl	0.4082
34	32/45	p. YFl	p. p. Y	no change	0.4694
35	71/36	w. Ab	w. Y	p. YFl	0.3673
36	79/42	w. Ab	w. Y	p. YFl	0.3878
37	37/38	w. Ab	Y	no change	0.3265
38	74/19	-	p. BFl	no change	0.1837
39	67/13	-	p. BFl	no change	0.1224
40	23/32	p. YFl	w. Y	no change	0.8061
41	-	Ab	w. Y-O	no change	0.4592
42	20/63	p. YFl	no change	no change	0.3980
43	73/42	-	p. B-GFl	no change	0.5918
44	-	-	-	p. BFl	0.0408
45	78/30	p. BFl	no change	no change	0.3908
46	-	YFl	no change	no change	0.0510
47	12/77	p. YFl	no change	no change	0.6429
48	39/80	p. BFl	p. GFl	no change	0.4898
49	41/71	Ab	Y-G	no change	0.1735
50	77/29	WFl	v. p. YFl	no change	0.1327
51	36/54	v. p. YFl	p. Y	no change	0.4592
52	84/64	-	-	B-GFl	0.2551
53	64/88	p. BFl	no change	no change	0.1224
54	75/73	p. B-GFl	no change	no change	0.1735
55	41/47	W-BFl	no change	no change	0.0612
56	52/63	-	-	YFl	0.2347
57	57/99	GFl	no change	no change	0.0204
58	54/85	w. BFl	W-GFl	no change	0.1024
59	54/19	Y-GFl	no change	fades out	0.0714
60	58/56	p. B	no change	no change	0.0714

[1] Key: b.=bright; p.=pale; v.=very; w.=weak; B=blue; G=green; O=orange; P=purple; W=white; Ab=absorption; Fl=fluorescent.
[2] Tertiary-butyl alchohol-acetic acid-water, 3:1:1/15 percent acetic acid.
[3] The proportion of individual plants in which the phenolics were found.

characterized (Table 2). Of these compounds, 14 were found in all specimens sampled, and 15 occurred in more than 75 percent of the experimental plants. These, plus an additional compound (number 30 of Table 2), occurred in relatively high concentrations and were easily detected. The 30 remaining compounds occurred in small concentration and their "absence" may well have reflected our inability to detect them. If, however, detectability is a true indication of the presence or absence of these minor oak phenolics, an interesting correlation exists between the results of our analysis and an observation made by Muller (1952), that species of oak are notoriously variable in trivial characters.

The determination of the similarity indices followed the method used originally by Sokal and Sneath (1963), with modifications to take care of variation in sample size (Taylor, 1971). The basic formula used for calculation of the similarity indices (SI) is:

$$SI = \frac{\text{similarities}}{(\text{similarities} + \text{dissimilarities})}.$$

A similarity was the occurrence of a common compound in two specimens being considered; a dissimilarity resulted from the occurrence of a compound in one of the plants and not in the other. A compound not occurring in either of the specimens was not considered in the determination of similarity. It is emphasized that the dissimilarities between the specimens were based primarily on minor compounds and may therefore be exaggerated.

The individual plants were clustered on the basis of similarities and from this cluster analysis, a phenogram was derived (Fig. 2). The phenogram reflects the close chemical similarity of the plants sampled in July and August (the original population or Group I of the phenogram). The significance of this grouping is that the environmental modifications are greater than those due to genetic variation, in spite of the fact that somewhat questionable minor characters were included in the analysis. In other words, the similarity between those plants collected in July and August, despite their different localities, exceeded that between plants sampled from the same site, or even the same plants, but at different times. This phenomenon was previously reported for *Tiarella*, a small herbaceous plant (Taylor, 1971).

The other groups of the phenogram tend to show geographical correlations but with several exceptions (see the explanation of Fig. 2). These correlations do imply that the detected presence or absence (or concentrations) of the minor pigments are either genetically controlled and differ somewhat between populations, or the environment of a given locale tends to cause chemical similarities within a population.

Discussion

The recent history of oak communities of Washington probably parallels that of the Willamette Valley of Oregon as described by Sprague and Hansen (1946), Habeck (1961), and Thilenius (1968). These investigators emphasized the role of competition (especially on deep loam soils) with faster growing conifers in structuring oak forests, and of fire in maintaining savanna-like "oak openings." Washington

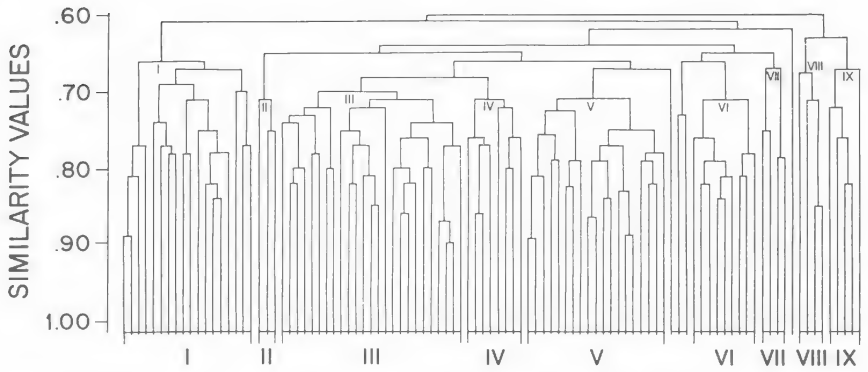


Figure 2. Phenogram showing similarity pattern among individuals and groups of *Quercus garryana.* Each line originating from the base represents a single specimen. The similarities are based on nearest-neighbor analysis.

Group I includes plants collected in July and August, 1973, and involves statewide distribution. Two plants of October collections included within this group are one from Sucia Island (San Juan County) and one from Bellingham (Whatcom County). *Group II* includes three specimens from well-separated locations in western Washington (San Juan Island, Oakville, and Bellingham). *Group III* is a heterogenous representation centered around the Columbia River (Klickitat, Skamania, and Clark counties) with a few "outcasts" from western Washington (Grays Harbor and Lewis counties) and two specimens from Oakville (Grays Harbor County), with one specimen from Corvallis and another from Satus Pass (Yakima County). *Group IV* consists of six specimens from Oakville and one from each of Lewis and Clark counties. *Group V* is another heterogenous assortment with most complete representation from southwestern Washington, especially Washougal River (Clark County) and Oakville, with individual specimens from Skamania and Klickitat counties and "outcasts" from Pierce and Yakima counties. *Group VI* consists of specimens from Satus Pass with a few individuals from Skamania, Klickitat, and Clark counties. *Group VII* includes four specimens from Satus Pass. *Group VIII* is a mixed group of five plants from Satus Pass, Oakville, and Trout Lake (Klickitat County). *Group IX* consists of three plants from Satus Pass and two from the Washougal River populations. In general, exclusive of Group I and the many exceptions noted above, the pattern of similarities from left to right in the phenogram corresponds to the geographical distribution of oak, from western Washington, through the Columbia Gorge, to south-central Washington.

communities tend to be small and disjunct, often occurring as scattered relics or limited groves. In some areas, e.g., Satus Pass, the communities appear to exist as clones, at least in part, spreading by root sprouts.

The associated vegetation is also similar to that of the Willamette Valley as discussed by Thilenius. On the loam soil of the Washougal River Valley, the forest was dense and dominated by oak and Oregon ash (*Fraxinus latifolia*). *Symphoricarpos alba* and *Rhus diversiloba* were common members of the shrub stratum. On Satus Pass, the oak forest was generally open with a grass understory. In the drier and rockier sites, oak was often mixed with ponderosa pine (*Pinus ponderosa*), while in more desirable habitats Douglas fir (*Pseudotsuga menziesii*) was a strong competitor. In the third large community sampled, Oakville, oaks occurred in a mixed forest with Douglas fir and western hemlock (*Tsuga heterophylla*). Here the shrub stratum was diverse and well developed, containing such species as *Symphoricarpos alba, Holodiscus discolor, Acer circinata,* and others. Various weedy species were common throughout the oak communities, reflecting a high degree of disturbance.

The original derivation of oak forests in Washington is uncertain. As previously stated, morphological parameters showed little or no correlation with distributional patterns. Although there is some relationship between distribution of plants and their phenolic similarities, as reflected by the phenogram (Fig. 2), the correlation is not statistically significant. However, the most widely accepted hypothesis for the origin of the Washington oak forests is that they migrated up the Willamette Valley with the drying and cooling climates of the late Tertiary and were split by the Washington Cascade Range. The western element followed the Puget lowland climatic belt to southern British Columbia and the San Juan islands. The eastern element migrated through the Columbia Gorge to south-central Washington. The phenogram shown and discussed in Figure 2 weakly reflects this migratory pattern.

We would like to present another interesting and provocative explanation for the distributional patterns—anthropological influence. It is generally assumed that many secondary metabolites, such as flavonoids, serve nonvital or nonspecific roles in the life of a plant and are therefore expressions of free mutations. If the present populations are remnants of a more extensive and continuous oak forest, it might be expected that phenolic patterns of individuals within populations should be very similar and those of isolated populations should be more distinct. This is especially true in such small breeding populations with random drift possibilities and decrease of genetic variability due to inbreeding and cloning. (It is acknowledged that isolation does not automatically lead to morphological or chemical divergence, but certainly it is considered to be the primary factor in such divergence.) The intrapopulational similarity would undoubtedly be greater with a more accurate method of resolving minor pigments. Given this high degree of apparent genetical similarity among the Washington oaks, the problem of dispersal of heavy acorns and short-term acorn viability, and the pattern of distribution, it does not seem unreasonable that in Washington man has been a vector in the dispersal of oaks from a common source. Indians of the Pacific Northwest used acorns in the making of bread and other foodstuffs and traded rather freely with one another. During the summer the tribes from eastern Washington (Klickitat, Yakima, Kittitas) crossed the Cascades, using the Cowlitz, Snoqualamie, and Naches passes, as well as the Columbia Gorge, to trade with tribes from western Washington. Tribes from Washington also intermarried. The Satsop, Puyallup, and Skykomish Indians of the Puget Sound area intermarried, while the Nisqually of Puget Sound exchanged mates with the Klickitat, east of the Cascades. Also, many tribes frequently relocated their villages far from the sites of older ones. For example, the Clallam Indians moved from Sequim, on the Olympic Peninsula, and founded a new village on Vancouver Island. (Information concerning Indian habits and village locations was taken from Haeberlin and Gunther, 1930; Seaman, 1945; Swarton, 1968; and Dorothy Neil, personal communication, 1974.)

Such trading parties, intermarriages, and relocation of villages may be responsible for the indigenous populations of oaks in the state. Many sites where Garry oak is found, especially in the San Juan Islands, Columbia Gorge, and eastern Washington, are the locations of former Indian villages. This close correlation is reflected in Figure 1 (see also Table 3). Of course, it is entirely possible that cause and effect have been reversed in the above discussion and that the Indians established their villages in or around existing oak forests.

TABLE 3. Indian villages—oak relationships.

Indian Tribe	Village[1]
Swallah	San Juan and Orcas Islands S.E. end of Orcas East side of San Juan Waldron Island
Swinomish	Whidbey Island Penns Cove Oak Harbor
Cathlamet	just east of Oak Point—mouth of Coal Creek
Chehalis	Westport near Centralia
Clallam	Sequim later—Vancouver Island, Beecher Bay
Lummi	Orcas Island Marietta
Samish	Samish Bay Guemes Island
Satsop	Satsop River
Skilloot	Oak Point
Twana	Oak Head—Hood Canal to Port Gamble mouth of Skokomish
Wishram	one mile below Wishram
Yakima	Satus Creek Naches River
Watala	Washougal River just below Cascade Rapids
Nisqually	Yelm near Roy South Tacoma Olympia

[1] Distribution of Indian villages follows Swarton (1968). See Figure 1 for distributional patterns of Indian villages.

Literature Cited

Axelrod, D. I. 1958. Evolution of the Madro-tertiary Geoflora. Bot. Rev. 24: 433-509.

Grant, V. 1971. Plant Speciation. Columbia University Press, New York.

Habeck, J. R. 1961. The original vegetation of the mid-Willamette Valley, Oregon. Northwest Sci. 35: 67-77.

Haeberlin, H., and E. Gunther. 1930. The Indians of Puget Sound. University of Washington Press, Seattle.

Muller, C. H. 1952. Ecological control of hybridization in *Quercus*: A factor in the mechanism of evolution. Evolution 6: 147-161.

Seaman, N. G. 1946. Indian Relics of the Pacific Northwest. Binfords & Mort, Portland, Oregon.

Sokal, R. R., and P. H. A. Sneath. 1963. Principals of Numerical Taxonomy. W. H. Freeman & Co., San Francisco.

Sprague, F. L., and H. P. Hansen. 1946. Forest succession in the McDonald Forest, Willamette Valley, Oregon. Northwest Sci. 20: 89-98.

Swarton, J. R. 1968. The Indian Tribes of North America. Smithsonian Institute Press, Washington, D.C. (2nd edition).

Taylor, R. J. 1971. Biosystematics of the genus *Tiarella* in Washington Cascades. Northwest Sci. 45: 27-37.

Thilenius, J. F. 1968. The *Quercus garryana* forests of the Willamette Valley, Oregon. Ecology 49: 1124-1133.

Tucker, J. 1953. Two new oak hybrids from California. Madroño 12: 119-127.
U.S. Department of Agriculture. 1965. Silvics of Forest Trees of the United States. Agricultural Handbook #271, U.S. Forest Service, pp. 595-599.

Received July 19, 1974.
Accepted for publication December 12, 1974.

Association News

The annual meeting of the Association was held at Central Washington State College on March 28 and 29 under the very able leadership of President John Shrader. There were about 200 registered for the meeting, and the various sections reported good programs and attendance. Two special features, a film festival and an energy symposium, were both well received by those in attendance.

New officers elected were:

President—Ernest Gilmour, Eastern Washington State College
Vice President—Kenneth Holmes, Oregon College of Education
Secretary—Milton Mosher, Washington State University
Treasurer—Richard Naskali, University of Idaho

New Trustees elected were:

Randall Brown—Consultant
D. P. Lavender—Oregon State University
Frank Nicol—Eastern Washington State College
Don Ringe—Central Washington State College
J. G. H. Smith—University of British Columbia

New Honorary Trustees named were:

Philip Haddock—University of British Columbia
P. Marshall—Eastern Washington State College
A. E. Weissenborn—Geological Survey

Honorary Life Members named were:

Rexford Daubenmire—Washington State University
D. J. Wort—University of British Columbia

Research grants were made to:

Newell Campbell—Yakima Valley College ($150)
Tim Clark—University of Wisconsin ($100)
Sandra Johnson—University of Montana ($100)
Jacob Rajala—Washington State University ($100)

Members present at the business meeting voted to increase dues for regular members from $5 to $7 and for student members from $2 to $3, with a $1 surcharge to be assessed if dues are not paid before January 1, 1976. New members can always join at the lower fee (no surcharge).

A constitutional change to include a dissolution section as required by IRS will be placed before the membership.

The 1976 annual meeting of the Association will be held in late March at Eastern Washington State College in Cheney. A special feature of this meeting will be a scabland symposium.

Thomas A. Leege
Idaho Fish and Game Department
Kamiah, Idaho

and

William O. Hickey
Idaho Fish and Game Department
Salmon, Idaho

Growth and Dieback of Redstem (Ceanothus sanguineus) in Idaho

Abstract

Annual growth and dieback of redstem ceanothus was influenced by weather, aspect, elevation, and plant age. The length of annual twig growth was strongly correlated with the amount of precipitation during the period of May through August ($r = .90$). Substantial dieback occurred when minimum daily winter temperatures dropped rapidly to less than 0°F. Dieback was greatest on old redstem plants, especially those that were weakened from the stresses associated with advanced forest succession.

Introduction

Redstem ceanothus (*Ceanothus sanguineus*) constitutes about one-third of the winter diet of elk (*Cervus canadensis*) in the Lochsa River drainage (Trout and Leege, 1971). Undoubtedly, it is a very important winter browse for elk throughout northern Idaho and adjacent areas of Washington and Montana.

Twig growth on many shrub species varies significantly from year to year. Researchers have found a strong relationship between annual twig length and precipitation (Garrison, 1953; Shepherd, 1971; Halls and Alcaniz, 1972, and others), but the important period of precipitation has varied with the shrub species and weather patterns in the study area. No information about the growth-precipitation relationships for redstem has been reported.

The woody tissue of shrubs sometimes withers and dies, frequently in response to rapid fluctuations in air temperature. The twig growth that is lost in this manner is referred to as dieback and is commonly found on many species of *Ceanothus.* Young and Payne (1948) reported that about 15 percent of the new redstem growth in northern Idaho was killed by a severe frost in late May, 1942. Stickney (1965) documented a large dieback of snowbrush (*Ceanothus velutinus*) during the winter of 1962-63 in the Missoula, Montana, area and suggested that it was caused by a severe drop in temperature following a mild period. Williams (1963) reported substantial redstem dieback in northern Idaho during the same winter, but he did not suggest a cause.

In this paper we relate the annual growth and dieback of redstem to weather, site characteristics, and plant age. The word "significant," when used in reference to specific findings, indicates statistical probability at the 0.05 level.

Methods and Study Area

In the fall of 1966 and during the next four years, we tagged and measured redstem annual growth on east, south, and west aspects at 2000 ft, 3000 ft, and 4000 ft (610 m, 915 m and 1220 m, respectively) and on a north aspect at 4000 ft in the Pete King Creek drainage, a tributary of the Lochsa River in northern Idaho. At each site we selected 20 plants in a systematically random manner and measured the annual growth on one branch of each plant. Each branch was selected on the basis of having three to six unbrowsed twigs that did not exhibit any dieback and were less than 7 ft (2.1 m) above the ground, an arbitrary height related to browse availability. We returned to these transects each spring, usually in April, and measured the amount of the past year's stem growth on browsed and unbrowsed twigs that had died since the fall measurement. We measured to the nearest 0.5 in (1.27 cm) the growth and dieback of about one thousand twigs annually, for five years and four years respectively.

All study sites occurred within the *Abies grandis-Pachistima* or *Thuja plicata-Pachistima* habitat types as described by Daubenmire and Daubenmire (1968). Soils were of a granitic origin and slopes ranged from 40-90 percent. Annual precipitation averaged 38 in (96 cm) at 2000 ft and increased to about 45 in (114 cm) at 4000 ft. Nine of the study sites were burned by wildfire in 1934, and vegetation ranged from relatively open shrub stands on the xeric exposures to advanced conifer regeneration on moister aspects. Four other sites, all at 4000 ft, were clearcut-logged in 1961 and broadcast-burned in the fall of 1962. Since fire is the primary agent which stimulates germination of redstem seeds, we assumed that the plants we measured on the 1934 burn sites ranged from 32 to 36 years old during the five year study. Likewise, plants in the clearcuts ranged from four to eight years old. Throughout this paper we refer to these redstem as old and young plants, respectively. Whenever young and old plants are compared, we are referring only to the plants at 4000 ft, as all of the young plants occurred at that elevation in the clearcuts.

Results and Discussion

Annual Growth

The length of the average current annual growth twig for five growing seasons on old redstem plants varied from a low of 9.3 in (23.6 cm) in 1970 to a high of 12.0 in (30.5 cm) in 1968 (Fig. 1). We calculated correlation coefficients for precipitation and growth for all combinations of months, including those of the previous growing season, and found the May-through-August period to have the highest relationship ($r = .90$) with annual growth. A regression equation of: $5.77 + 0.633$ (total in ppt. for May through August) estimated average annual leader length in inches. May and June are typically wet months, whereas July and August are very dry. Annual growth began in May and usually terminated in July, unless adequate precipitation fell during July and August to prolong the growing period. This was the case in 1968 when both July and August precipitation was above average. The sample size was much smaller for young plants, so a correlation between twig length and precipitation was not computed.

On young plants, length of annual growth did not differ significantly among all

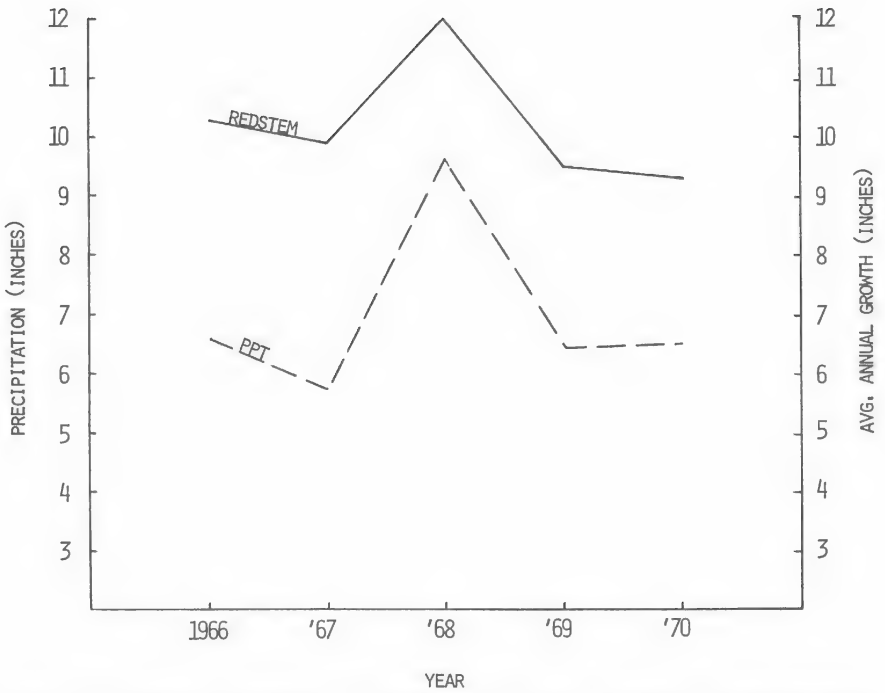


Figure 1. Relationship of redstem annual growth (old plants) to precipitation during the May-through-August period.

four aspects during the five year period. However, the length of the annual growth twigs on old plants was significantly greater on the south aspects (Table 1).

There was no apparent relationship between elevation and growth. Twigs were longest at 2000 ft for two years, at 3000 ft for one year, and at 4000 ft for two years.

Dieback

Dieback was divided into two types—that which occurred on a twig after it was browsed upon (browsed dieback), and that which occurred with no apparent twig injury (unbrowsed dieback). Browsed dieback on both young and old redstem plants averaged 3.5 percent of the linear annual growth and ranged from 2.9-4.6 percent

TABLE 1. Mean annual twig length in inches for old plants (32-36 years old), on three aspects.[1]

Year	South	East	West	Average
1966	10.9	10.6	9.5	10.3
1967	11.5	9.5	8.7	9.9
1968	12.2	11.9	11.9	12.0
1969	9.8	8.2	10.4	9.5
1970	12.6	8.7	6.7	9.3
Average	11.4[2]	9.8	9.4	10.2

[1] Each measurement is an average from 3 transects, 1 each at 2000 ft, 3000 ft, and 4000 ft.
[2] Significantly different from east and west aspects at 0.05 level.

during the four years. About 38 percent of the annual growth twigs were browsed upon during this period. We noted that as the percentage of browsed twigs increased, the percentage of browsed dieback also increased. Unbrowsed dieback averaged 5.9 percent annually, and deviated significantly from this mean during only one winter, 1968 to 1969, when almost two and one-half times as much unbrowsed dieback (12.9 percent) occurred as during the next highest year (5.2 percent).

Stickney (1965) suggested that a warm period of five to ten days with maximum temperatures 5-10° F above freezing and minimum temperatures not more than 5° F below freezing may change the winter hardiness of *Ceanothus velutinus*. He speculated that if such a period is followed by a sudden drop in temperature to 20-35° F below freezing in 24 to 48 hours, frost damage may occur. During the four years of our study, a temperature fluctuation similar to this occurred only during late December, 1968, the winter of greatest redstem dieback. The average maximum daily temperature for December 15 to December 28 was 36.6° F (2.6°C) and the daily minimum was 24.9° F (-3.9°C) at Fenn Ranger Station, about 1600 ft in elevation and eight air-miles (12.9 km) from the study plots. On December 29, the temperature dropped sharply, and for the following three days the average maximum temperature was 15° F (-9.4°C) and the average minimum was -4 F° (-20°C). The lowest temperature was -12° F (-24°C) on December 31.

Williams (1963) reported a large dieback for redstem during the winter of 1962 to 1963 on study areas within 25 mi (40 km) of ours. Weather records for that period from Fenn Ranger Station (U.S. Dept. of Commerce, 1962) indicate that a rapid decrease in temperature occurred in late December when the minimum daily temperature dropped from 28° F (-2°C) to -10° F (-23°C) in two days. Six days later it warmed to a minimum temperature of 31° F (-6°C) and then cooled to -4° F (-20°C) in the following two days. Therefore, similar temperature fluctuations in both 1962 and 1968 resulted in larger than normal amounts of dieback. During both years, when the cold temperatures occurred, there was less than one foot (30 cm) of snow on the ground below 4000 ft elevation. Additional quantities of snow may have reduced dieback by insulating portions of the plant from the severe temperature fluctuations.

It would seem that dieback caused by temperature fluctuations should have been more severe on south aspects because of greater insolation, and thus higher temperatures during the daytime, with night temperatures equally low as those on other aspects. In addition, snow depths were less on south exposures, and more of each plant was exposed to temperature extremes. This pattern of dieback did occur on the young plants as they had significantly more unbrowsed dieback on the south exposure than the other aspects. However, the unbrowsed dieback on old plants was significantly greater on the east aspect (Fig. 2).

There was significantly more unbrowsed dieback on old plants than on young plants during each winter (Fig. 3). Unbrowsed dieback on old redstem was usually greater (but not significantly so) at low elevations than at high elevations. However, Williams (1963) found the opposite to be true as dieback increased from about 27 percent at 2000 ft to 56 percent at 4000 ft during the winter of 1962 to 1963.

Although we recorded information regarding dieback only on annual growth twigs, we noted that in some instances branches and even entire plants were killed at ground level. Sometimes, the plant responded by sprouting from the root crown.

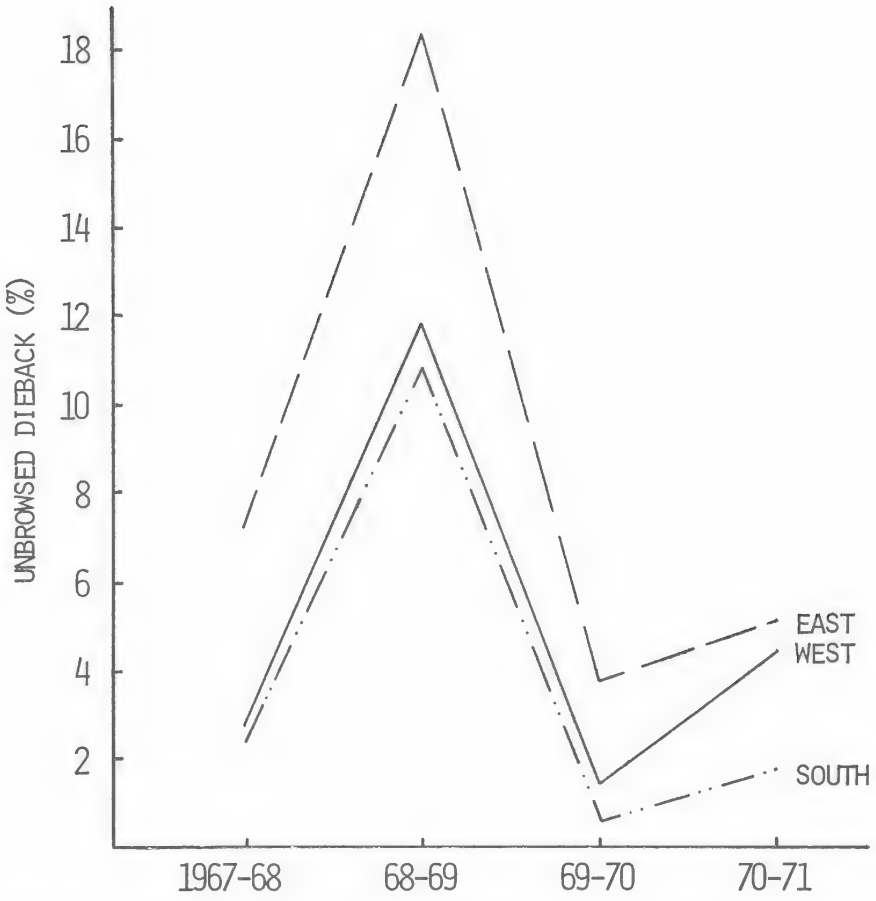


Figure 2. Relationship of unbrowsed dieback of annual growth (old plants) to aspect.

Effects of Plant Succession

Shading of the understory increases as plant succession advances toward the conifer climax. The rate of succession is affected by available moisture, which in turn is influenced greatly by exposure to the sun, especially where slopes are steep. Consequently, north aspects are the wettest and plant succession there is the most rapid (Fig. 4). Conversely, south aspects are the driest and their succession the slowest. East aspects are somewhat wetter than west aspects.

On our study area, redstem (young) germinated and grew very well on all four aspects at 4000 ft elevation after mature stands of *Abies grandis* and associated conifers were clearcut-logged and the slash broadcast-burned. However, at the same elevation on an adjacent area where mature timber was burned by wildfire in 1934, live redstem (old) plants were absent on north aspects, scattered on east and west aspects, and numerous on south aspects. Dead plant crowns indicated that redstem had been

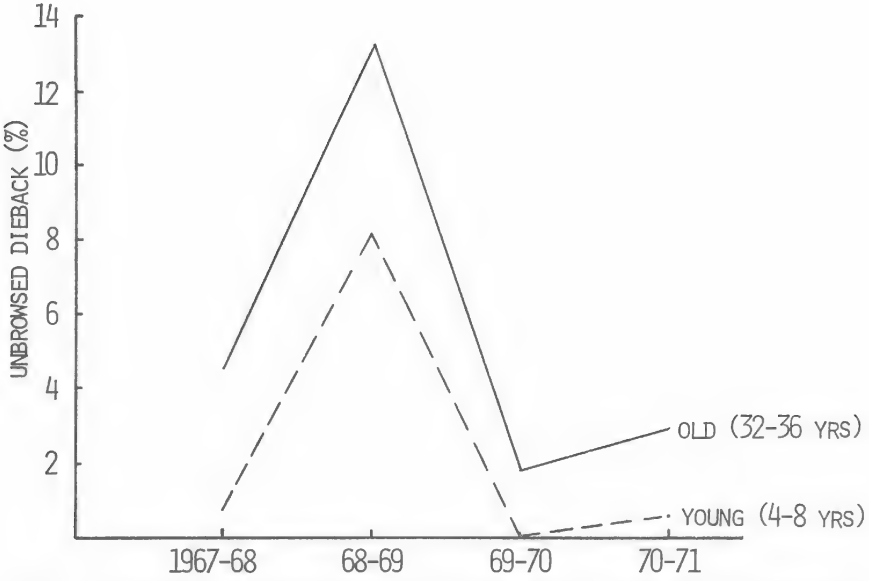


Figure 3. Relationship of unbrowsed dieback of annual growth to plant age, at an elevation of 4000 ft.

Figure 4. A small tributary of the Lochsa River that was burned by wildfire in 1919 and 1934, and photographed in 1969. Plant succession toward the conifer climax is occurring at a much faster rate on the northerly exposure.

more abundant at one time on all aspects, especially the northern, eastern, and western. It appears, then, that the density of the old redstem plants is closely related to shadding. This is further indicated by our data which suggest that plant vigor is diminished as shade increases. The young plants were still completely exposed to sunlight on all four aspects as succession was not far enough along for other plants to overtop them. Average twig lengths were about the same on all aspects. However, on the old plants, twig lengths were longest on the south aspect, probably indicating that the increased shade had reduced vigor of plants on the other aspects.

Differences in amounts of unbrowsed dieback also support this hypothesis. The young plants showed the expected pattern of dieback when plants on all aspects were of equal vigor. However, the old plants showed greater dieback on east and west aspects, rather than south, during every year of the study. If there had been any old plants alive on north aspects, they probably would have suffered the greatest dieback. It appears, then, that dieback associated with extreme temperature fluctuations acts as a mechanism for removing redstem from the plant community, especially where plant vigor has been reduced by the shading associated with advanced succession.

Acknowledgements

This study was financed by Idaho Federal Aid Project W-139-R. We acknowledge the assistance of J. L. Gifford, G. D. Power, T. A. Meske, M. L. Orme, and M. W. Schlegel of the Idaho Fish and Game Department, who assisted with field work, data compilation, and manuscript review. We are grateful to Dr. J. R. Nelson, Washington State University, for criticizing the manuscript.

Literature Cited

Daubenmire, R., and Jean B. Daubenmire. 1968. Forest Vegetation of Eastern Washington and Northern Idaho. Washington State Univ. Agr. Exp. Sta. Tech. Bull. 60, 104 p.

Garrison, G. A. 1953. Annual fluctuation in production of some eastern Oregon and western Washington shrubs. J. Range Manage. 6(2): 117-121.

Halls, L. K., and R. Alcaniz. 1972. Growth Patterns of Deer-Browse Plants in Southern Forests. South. For. Exp. Sta. Res. Paper SO-75. 14 p.

Shepherd, H. R. 1971. Effects of Clipping of Key Browse Species in Southwestern Colorado. Colo. Div. of Game, Fish, and Parks. Tech. Pub. No. 28. 104 p.

Stickney, P. F. 1965. Note on winter crown kill of *Ceanothus velutinus*. Proc. Mont. Acad. Sci. 25: 52-57.

Trout, L. C., and T. A. Leege. 1971. Are the northern Idaho elk herds doomed? Idaho Wildl. Rev. 24(3): 3-6.

U.S. Dept. of Commerce. 1962. Climatological Data—Idaho 65(12).

Williams, T. R. 1963. Lochsa Elk Study. Job Completion Rep., W-85-R-14, Job No. 12, Ida. Fish and Game Dept. 24 p.

Young, V. A., and G. F. Payne. 1948. Utilization of "key" browse species in relation to proper grazing practices in cutover white pine lands in northern Idaho. J. For. 46(1): 35-40.

Received December 27, 1974.
Accepted for publication February 7, 1975.

Stuart E. Nixon
Department of Biology
Western Washington State College
Bellingham, Washington

The Ecology of Deadhorse Cave

Abstract

A lava cave of south central Washington, Deadhorse Cave, is described along with four cave organisms which exhibit varying degrees of cave adaptation. Various chemical and biological parameters of the cave were measured at different seasons.

Lava caves of the Pacific Northwest have been virtually overlooked by biospeleologists, even though these caves possess fauna which exhibit cave adaptations. Some papers have described new species of cave organisms, but little has been mentioned of the cave environment itself. An overview of some of the important species that are found in various regional caves was presented by Peck (1973). In the study presented here, four cave organisms have been studied and their particular cave adaptations described.

Lava caves, like limestone caves, can be considered isolated ecosystems, in that they often restrict gene flow between populations to the extent that factors such as genetic drift and inbreeding can affect the evolution of representative fauna. If isolation from surface populations is maintained for a sufficiently long time, these factors of genetic drift and inbreeding, along with natural selection, can cause sufficient divergence to bring about speciation. The analogy by Culver (1970) of caves to islands is applicable and appropriate to Deadhorse Cave, a lava cave of south central Washington discussed in this paper.

Deadhorse Cave is located in Skamania County, approximately seven miles northwest of Trout Lake. The cave is immediately south of road N88, and west of Deadhorse Creek. The cave was formed by a surface pahoehoe lava flow in the Mt. Adams area, and although the cave's existence has been known for some years, no extensive exploration or mapping was done until 1969 (Nieland, 1971).

As with many of the entrances of caves in this area, the lower entrance to Deadhorse Cave is a sink which was formed when parts of the ceiling collapsed. The upper entrance is an air hole, located approximately 1,000 ft uphill from the lower entrance. The cave has numerous lava features characteristic of this area, such as multiple passage levels, stalactites, extensive breakdown, and laval seals. The cave differs, however, in that it exhibits a complex network of passages, many on different levels, with numerous side branches. The cave was formed on the side of a hill, and this unusual characteristic may explain the irregular pattern of lava flow.

Numerous pools of water are located in the cave, some arising from springs and some formed by water dripping from the ceiling and seeping from the walls. This large amount of seepage causes the interior of the cave to be extremely damp throughout the year. A stream in the central part of the cave feeds pools of water at various locations along its length, and a spring approximately 100 ft from the lower entrance feeds a small pool which varies in size throughout the year.

Materials and Methods

Field trips to the cave were made on October 21, 1973, March 27, 1974, and July 6, 1974. On the first trip the lower pool was approximately 8 ft long, 2 ft wide, and varied from 2-12 in in depth. Aquatic organisms were collected from the pool, and water samples were taken for chemical and bacteriological studies. Within 24 hours the samples were analyzed for concentrations of dissolved oxygen, carbon dioxide, carbonates, and chlorides, using standard techniques (see Welch, 1948). Titration reagents used for the determinations were 0.025 M $Na_2S_2O_3$ for oxygen, 0.010 M NaOH for carbon dioxide, 0.010 M HCl for carbonates, and 0.010 M $AgNO_3$ for the chlorides. Measurement of pH was made in the field, using Van Waters and Rogers pH paper, and air and water temperatures were taken. Serial dilutions were made from the samples, and bacteria were cultured using nutrient agar as the growth medium. Bacterial cultures were grown for 24 to 48 hours, and plates containing between 50 and 200 colonies were counted. Soil was very sparse throughout the cave and was seldom more than an inch in depth. A few soil organisms were collected and were preserved in ethyl alcohol.

During March, the passage was filled with water to a level approximately 75 ft from the lower entrance. Aquatic organisms were collected at this location, and water samples were again taken and analyzed. In July, the water level had receded sufficiently to allow passage through the cave, although the level was still much higher than in October. Aquatic organisms were collected from the lower pool, as well as from a pool in a major side branch of the main passage. Water samples were taken and measurements were made of the pH and temperatures as before.

Results and Interpretations

Chemical and Bacteriological Studies

Concentrations of the dissolved gases and ions, along with the pH, water and air temperatures, and bacterial counts, are listed in Table 1. Six countable plates (those containing between 50 and 200 colonies) were obtained in October, five in March, and five in July. The number reported in Table 1 is the average of these countable plates.

The large increase in volume of water in the lower end of the cave between October and March obviously affected some of the characteristics of the lower pool. Indeed, the small pool was transformed into a sizable lake with a much smaller

TABLE 1. Various chemical and biological parameters of the lower pool of Deadhorse Cave measured at different seasons.

Parameters	October 21, 1973	March 27, 1974	July 6, 1974
Air Temperature	7°C.	6°C.	6°C.
Water Temperature	5°C.	4°C.	4.5°C.
pH	5.0 ± .5	4.5 ± .5	4.5 ± .5
Dissolved O_2 Content (ppm)	23 ± 4	13 ± 4	16 ± 4
Dissolved CO_2 (ppm)	40 ± 5	10 ± 2	29 ± 3
$CO_3^=$ (ppm)	56 ± 5	33 ± 3	34 ± 3
Cl^- (ppm)	0.0012 ± .0005	0.0010 ± .0005[1]	0.0017 ± .000
Bacteria (bact/ml)	9,500 ± 500	1,250 ± 500	7,500 ± 500

[1] All chemical measurements are averages of triplicate titrations except those marked with a superior figure which are averages of duplicates.

surface-volume ratio. The spring that fed the small pool in October imparted an appreciable amount of turbulence to the pool and thus provided substantial aeration in the shallow water. However, with the great increase in depth of the pool in March and July, this turbulent effect of the spring was far less pronounced. Relative movement of water, therefore, was considerably less in March and July than the movement observed in October: movement seemed negatively correlated with the increase in volume.

Classification and Description of Collected Organisms

Macroscopic aquatic and soil organisms collected are described individually below. Detailed morphological descriptions of three of these are already in the literature, and the reader is directed to the original papers if greater descriptive detail is desired. The fourth species is currently being studied by the author, and will be the subject of a later paper.

Phylum Arthropoda
Class Crustacea
Order Amphipoda
Family Gammaridae

Stygobromus elliotti Holsinger

This is one of 18 species of *Stygobromus* from western North America, all of which are found in caves or cave-like, freshwater habitats such as seeps and wells. This species found in Deadhorse Cave (its type locality) was recently described by Holsinger (1974). Like the other members of the genus, this species lacks eyes and pigmentation.

Three females were collected in October on the bottom of the lower pool. They were maintained in the laboratory for three to five months in darkness at 10° C. The largest individual had a body length of 8 mm. Antenna 1 was 4.5 mm in length with 19 segments on the primary flagellum and was approximately 50 percent longer than antenna 2. The second individual had a body length of 7.5 mm; antenna 1 was 4.3 mm in length with 19 segments on the primary flagellum, and was approximately 60 percent longer than antenna 2. The smallest individual collected had a body length of 6 mm; antenna 1 was 3.5 mm long with 17 segments on the primary flagellum, and was 45 percent longer than antenna 2. No individuals were seen in March, but in July many were observed in both the lower pool and in the side-branch pool mentioned above.

Phylum Arthropoda
Class Diplopoda
Order Chordeumida
Family Conotylidae

Troglotyla skamania Causey

Recently described by Causey (1972), this species has been found only in caves of the Mt. Adams area, and is the only species of the genus. (Deadhorse Cave is the type locality.) This species is a relatively large conotyloid millipede, the whole of which, including the ocelli, is unpigmented.

A single male specimen was collected in October from under a small stone, approximately 200 ft from the lower entrance. The body was 21 mm in length and 1.5 mm wide with 30 segments. Appendages of this species are not exceptionally elongated compared to epigean conotyloids. Millipedes generally are relatively conservative in cave adaptation (Causey, 1960).

Phylum Arthropoda
Class Insecta
Order Orthoptera
Family Grylloblattidae

Grylloblatta sp.

Nine species of *Grylloblatta* occur in the western United States and Canada. They live mainly in caves or under rocks in cool habitats, usually at high altitudes (Kamp, 1963). The body is thysanuriform and the general coloration is light yellow. The eyes are small and dark brown in color but lack ocelli. All species lack wings but are adapted for rapid movement, running much like a centipede (Walker, 1914).

Gurney (1961) has described *Grylloblatta chirurgica* from three caves of the Mt. St. Helens flow, approximately 20 miles west of the Mt. Adams caves. Most of the morphological characteristics of my specimens seem to be similar to those described by Gurney, but exact species determination has been difficult because only one adult specimen was collected.

A single nymph was collected in October from under a small stone in the central part of the cave. The body was 10 mm in length and had the characteristic straw-yellow coloration. Both antennae were 7.5 mm long and had 29 segments. The cerus was 4 mm long. An adult female and two additional nymphs, floating on the surface of the lower pool, were collected in March. They had obviously been flooded out from their preferred locations because two were dead and the third was struggling while being carried along by the slow movement of water.

The female had the following measurements: body length 18.5 mm, cercus 8.5 mm, and antennae 17 mm (with 34 segments, left, and 32 segments, right). Nymphs had body lengths of 8 mm and 12 mm, cerci of 3.5 mm and 4.5 mm, and antennae of 6.5 mm (with 34 segments on both) and 8.5 mm (with 28 segments, left, and 29 segments, right). Body color of the female was light tan and the head was light brown. The two nymphs were irregularly colored straw-yellow and white. Two additional nymphs were found floating on the surface of the lower pool in July but were dead and partially decomposed, which made detailed study impossible.

Phylum Platyhelminthes
Class Turbellaria
Order Tricladida
Family Planariidae

Polycelis coronata Girard

To date, cave planarians that have been described in North America have been from the family Dendrocoelidae (Hyman, 1939, 1954, 1956) and from three genera of the family Planariidae, *Phagocata, Kenkia,* and *Sphalloplana* (Hyman, 1937, 1939,

1945, 1954; Kenk, 1970; Mitchell, 1968). Hyman (1960) postulated that *Kenkia* and *Sphalloplana* may have evolved from *Phagocata,* and that the adhesive organ found in both *Kenkia* and *Sphalloplana* (but not *Phagocata*) and in many of the Dendrocoelidae may be the result of extensive parallelism.

Polycelis is only the fourth genus of Planariidae to be found in a cave, so its occurrence is of special interest. Exact species determination is uncertain at this time because none of the individuals collected were sexually mature. An additional complication is that no extensive study of freshwater flatworms has been undertaken in the state of Washington. Kenk (1973) indicates that only one species of *Polycelis* occurs north of California, and epigean specimens collected a few miles from the cave seem to be of this species, but as yet none have been sectioned. There seem to be a few differences, aside from the reproductive structures, between the cave form and the epigean specimens collected: the body pigmentation is lighter in the cave form, the eye spots are fewer in number, and the auricles are less pointed (see Fig. 1). These characteristics are not species-determining criteria, however, and until sexually mature individuals are collected, no conclusion can be made.

Nineteen individuals were collected in October, 7 in March, and 12 more in July. They ranged from 4 mm to 12 mm in length and were colored white to light tan. All were sexually immature when collected, and are presently being maintained in the laboratory in darkness at 10° C. The factors that induce sexuality are unknown, and, indeed, the constancy of the cave environment throughout the year may restrict maturity. A more complete study of the genus *Polycelis* in Washington is being undertaken by the author, and a future paper may shed more light on the variation

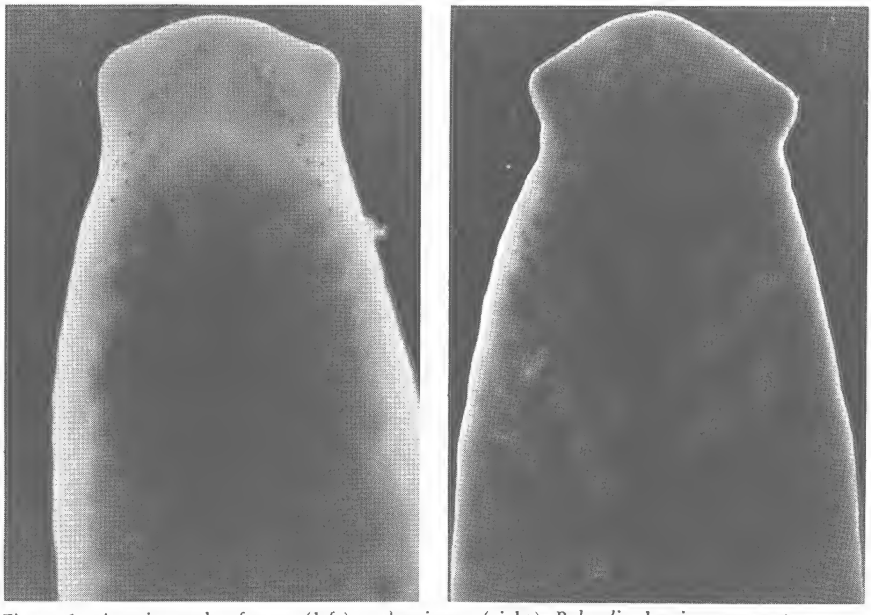


Figure 1. Anterior ends of cave (left) and epigean (right) *Polycelis* showing eye spots.

that exists in *Polycelis* in the Pacific Northwest and the possible speciation of the cave forms.

Acknowledgements

The author thanks R. J. Taylor for suggestions and criticisms of the manuscript, C. M. Senger for advice and comments on cave biology, and J. E. Erickson for assistance with the photographs.

Literature Cited

Causey, N. B. 1960. Speciation in North American cave millipedes. Am. Midl. Nat. 64(1): 116-122.

———. 1972. Two new conotyloid millipedes from Western North American and a key to the genus *Adritya* (Chordeumidae:Diplopoda). Proc. Louisiana Acad. Sci. 35: 27-32.

Culver, D. C. 1970. Analysis of simple cave communities I. Caves as islands. Evo. 24: 463-474.

Gurney, A. B. 1961. Further advances in the taxonomy and distribution of the Grylloblattidae (Orthoptera). Proc. Biol. Soc. Wash. 74: 67-76.

Hyman, L. H. 1937. Studies on North American triclad Turbellaria VIII. Some cave planarians of the United States. Trans. Am. Micros. Soc. 56: 457-477.

———. 1939. Studies on North American triclad Turbellaria X. Additional species of cave planarians. Trans. Am. Micros. Soc. 58: 276-284.

———. 1945. Studies on North American triclad Turbellaria XI. New, chiefly cavernicolous, planarians. Am. Midl. Nat. 34: 475-484.

———. 1954. Studies on North American triclad Turbellaria XIII. Three new cave planarians. Proc. U.S. Nat. Mus. 103: 563-573.

———. 1956. Studies on North American triclad Turbellaria 15. Three new species. Am. Mus. Novitates. 1808: 1-14.

———. 1960. Cave planarians in the United States. Am. Midl. Nat. 64: 10-11.

Holsinger, J. R. 1974. Systematics of the Subterranean Amphipod Genus *Stygobromus* (Gammaridae), Part I: Species of the Western United States. Smith. Cont. Zool., Number 160.

Kamp, J. W. 1963. Descriptions of two new species of Grylloblattidae and of the adult of *Grylloblatta barberi,* with an interpretation of their geographical distribution. Ann. Ent. Soc. Am. 56: 53-68.

Kenk, R. 1970. Freshwater triclads (Turbellaria) of North America, III. *Sphalloplana weingartneri*, new species from a cave in Indiana. Proc. Biol. Soc. Wash. 83: 313-320.

———. 1973. Freshwater Triclads (Turbellaria) of North America, V: The Genus *Polycelis*. Smith. Cont. Zool., Number 135.

Mitchell, R. W. 1968. New species of *Sphalloplana* (Turbellaria:Paludicola) from the caves of Texas and a reexamination of the *Speophila* and the family Kenkiidae. Ann. Spel. 23: 597-620.

Nieland, J. 1971. Deadhorse Cave, just another lava tube? Nat. Spel. Soc. News. 29: 142-144.

Peck, S. B. 1973. A review of the invertebrate fauna of volcanic caves in Western North America. Bull. Nat. Spel. Soc. 35(4): 99-107.

Walker, E. M. 1914. A new species of Orthoptera, forming a new genus and family. Can. Ent. 46: 93-99.

Welch, P. S. 1948. Limnological Methods. McGraw-Hill Book Co. 381 pp.

Received January 8, 1975.
Accepted for publication January 21, 1975.

David G. Fellin[1]

Research Forest Entomologist, USDA Forest Service
Intermountain Forest and Range Experiment Station
Ogden, Utah

Feeding Habits of Pleocoma[2] Larvae in Coniferous Forests of Western Oregon[3]

Abstract

Larval feeding habits of five species of *Pleocoma* were studied at a dozen forested sites in western Oregon.

Coniferous roots comprise the major part of the larval diet throughout most of the year, being found exclusively in 86 percent of the larvae. Thirty percent of the roots in larval guts were Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, often the predominant conifer at the collecting sites. Larvae preferred smaller roots, mostly 2 mm in diameter or less, many of them mycorrhizal rootlets. Some larvae merely girdled roots, but most larvae severed and consumed the entire root. Larvae either severed and ingested intact root segments or gnawed on root ends, masticating them before ingestion.

During most of the year, all larval stages at all depths were feeding on roots, with the exception of first and last instars, neither of which appear to feed on roots. Root-feeding ceases for at least two months during the moulting period between June and September. Most larvae consumed exuvia, and some soil was ingested by all larvae. Other material in larval guts was tentatively identified as: remains of fungal hyphae, cast ventricular epithelium, gregarine parasites and bacteria.

Pleocoma larvae do not appear to be a serious forest pest in old-growth coniferous forests primarily because larval populations are generally low and scattered. They are, however, a potential problem in newly established forests as seedlings can be killed by one or two larvae.

Although *Pleocoma* larvae have been known to be serious pests of orchard trees in the Hood River Valley for more than 20 years (Ellertson and Ritcher, 1959; Ritcher and Olney, 1953) and at The Dalles (Ellertson, 1956) in Oregon, evidence that *Pleocoma* larvae feed on roots of coniferous trees has been until recently only circumstantial. Adult *Pleocoma* often have been collected in and around Douglas-fir forests (Linsley, 1938, 1945; Hazeltine, 1952), and larvae of *P. conjungens* Horn have been taken within an area of yellow-pine roots (Hazeltine, 1950). (Yellow pine is a colloquialism for ponderosa pine, *Pinus ponderosa* Laws.) One collector's opinion is that larvae of *P. edwardsii* Le Conte normally feed on the roots of Douglas-fir (Linsley, 1957). It has been said of another species that: "Nothing at all is known about the feeding habits of *Pleocoma dubitalis dubitalis* larvae even though the species is found associated with Douglas-fir" (Ritcher and Beer, 1956).

The first confirmed record of *Pleocoma* larvae feeding on the roots of forest trees was in 1960. In February of that year, *P. simi* Davis larvae were discovered feeding

[1] Stationed in Missoula, Montana, at the Forestry Sciences Laboratory, maintained in cooperation with University of Montana.

[2] Coleoptera: Scarabaeidae.

[3] Technical Paper No. 3489, Agricultural Experiment Station, Oregon State University, Corvallis, Oregon. This investigation was supported chiefly by the Oregon Agricultural Experiment Station and National Science Foundation Grants Nos. 14296 and 17935 and partially by the Intermountain Forest and Range Experiment Station, USDA Forest Service. Based on portions of a dissertation submitted in partial fulfillment of the requirements of the Ph.D. degree in Entomology at Oregon State University.

on roots of 1- and 2-year-old conifer seedlings in experimental seedbeds located in a recently logged area east of Roseburg, Oregon (Stein, 1963).

The present study was conducted to determine the feeding habits of *Pleocoma* larvae under natural conditions in the soil of some old-growth coniferous forests in western Oregon. Five species of *Pleocoma* were studied—*P. dubitalis dubitalis* Davis (hereafter referred to merely as *P. dubitalis*), *P. carinata* Linsley, *P. simi, P. minor* Linsley, and *P. crinita* Linsley.

Materials and Methods

Larvae were collected from varied forested areas in western Oregon throughout the year. Larvae of *P. dubitalis* were collected once a month, from January through December 1961, in an old-growth Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, stand 8 km north of Corvallis. Larvae of *P. carinata* and *P. simi* were collected every 1½ to 2 months at various forested sites in southwestern Oregon, from June 1960 until December 1961. *Pleocoma minor* and *P. crinita* larvae were collected as time permitted in forested areas in the Hood River Valley.

Sample holes were dug in areas where *Pleocoma* was known to occur. Each hole was 1 m^2 and was dug no less than 75 cm deep but at least 15 cm deeper than where the last larva was found. Any hole dug to a depth of 75 cm without larvae being found was abandoned, and further holes were dug until a minimum of six larvae had been collected. As they were taken from the hole, larvae were placed at once into FAA. (Formalin-aceto-alcohol mixed as follows: ethyl alcohol (95 percent), 50 ml; glacial acetic acid, 10 ml; formalin (30-40 percent), 20 ml; distilled water, 35 ml.) At the laboratory, each larva was dissected, and a qualitative examination made of the contents of the alimentary canal. Gross dissections were made under a dissecting microscope with specimens pinned out under FAA. Gut contents were classified into one of four groups: roots, exuvia, soil, and other material. Root segments were measured and examined for type of damage done by the feeding larvae.

From each collection, six larvae were selected to represent the range in size of larvae and the range of depths over which they were collected. Stomodaea were removed intact from each larva, washed twice in 50 percent alcohol, dehydrated with dioxan, and embedded in paraffin. Embedded stomodaea were soaked in a glycerin-detergent solution for four to six weeks to soften the woody material, then they were sectioned immediately or stored in water under refrigeration.

Longitudinal serial sections of the stomodaea were cut at 10 μ on a rotary microtome, placed on glass slides, and stained with safranin and fast green. Each serial section was scanned under low magnifications to locate taxonomic features, which then were critically studied. Approximately 775 slides were prepared in order to identify all roots in the 150 *Pleocoma* stomodaea examined. Root fragments were categorized into three classes: gymnosperms, angiosperms, and ferns.

Indentification and Analysis of Gut Contents

Material found in the alimentary canals of more than 400 *Pleocoma* larvae included roots, larval exuvia, soil, and material tentatively identified as fungal hyphae, cast ventricular epithelium, and gregarine parasites.

Roots

Conifer roots were the most abundant material found in the guts of *Pleocoma* larvae; some guts were packed with roots, others contained only a trace of root fragments. Of 150 stomodaea, 131 contained gymnosperm roots (41 of which were Douglas-fir), 3 were full of angiosperm roots, 11 contained 2 classes of roots, and roots in 5 larvae were unidentifiable (Table 1). Angiosperms in six of nine larvae were

TABLE 1. Identification of roots from stomodaea of *Pleocoma* larvae collected in coniferous forests of western Oregon.

Identification of root	Number of larvae feeding on each class of root				
	P. dubitalis	*P. simi*	*P. carinata*	*P. minor* *P. crinita*	Total
Gymnospermae	42	23	19	6	90
Douglas-fir	24	11	4	2	41
Angiospermae Dicotyledonae			1		1
Oregon White Oak		1			1
Angiospermae Monocotyledonae			1		1
Gymnospermae-Angiospermae	1	3		2	6
Gymnospermae-Filicinae		1	4		5
Unidentifiable	3	1		1	5
	70	40	29	11	150

distinguishable only to class. Angiosperms in the remaining three larvae were identified as one monocot and two dicots (the monocot was identified as Oregon White Oak, *Quercus garryana* Dougl.). No stomodaeum contained exclusively fern roots, although fern roots were intermixed with gymnosperm roots in five stomodaea. The fern species on which the five larvae had fed probably was either bracken fern, *Pteridium aquilinum* (L.) Kuhn, or sword fern, *Polystichum munitum* (Kaulf.) Presl.

When more than one class of root was available, *Pleocoma* larvae probably fed on most roots with which they came in contact; the position of roots in some guts indicated that larvae exercised little selection since they appeared to ingest more than one class of root simultaneously or in close succession (Fig. 1). Though in addition to ferns and several coniferous species, several species of shrubs, such as golden chinquapin, *Castanopsis crysophylla* (Dougl.) A. DC., salal, *Gaultheria shallon* Pursh, and Oregon grape, *Berberis aquilfolium* Pursh, were growing at many sites, conifer roots were most abundant. The high incidence of gymnosperm roots in larval stomodaea no doubt reflects the abundance of these roots and does not indicate feeding preference.

On the other hand, when only conifer roots are available, *Pleocoma* larvae may exert some feeding selectivity. In a series of laboratory tests, I held *Pleocoma* larvae without food for several days, then offered them a choice of two species of freshly cut conifer roots. There was an indication that larvae preferred ponderosa pine to Douglas-fir and Douglas-fir to either incense cedar, *Libocedrus decurrens* Torr., or Oregon white oak. Stein (1963) reported that *P. simi* larvae damaged twice as many pine as firs when the two were equally available in experimental seedbeds; larvae appeared to reject incense cedar.

Pleocoma larvae fed on roots in several ways. More than one type of damage was usually found on individual roots. Many larvae followed roots through the soil and ate only the bark (phloem and all the tissues located outward from it) as they bur-

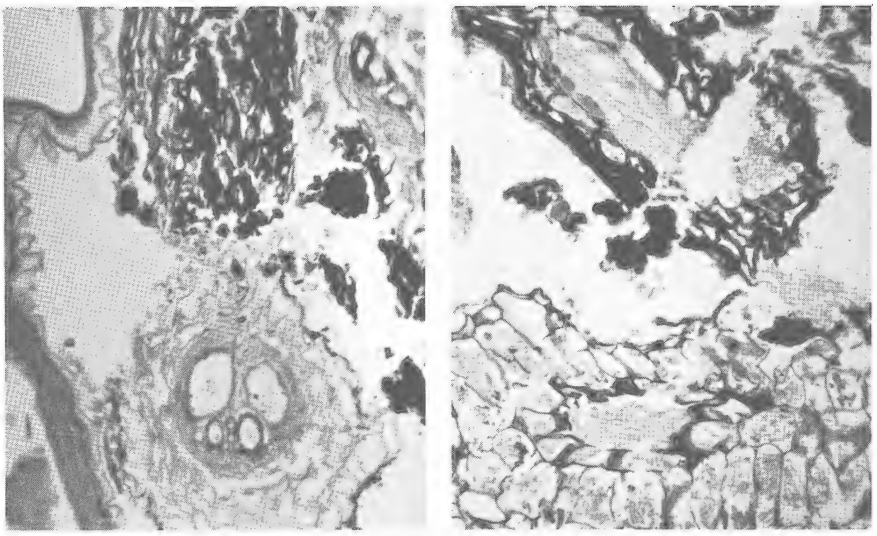


Figure 1. Photomicrographs showing two classes of roots in the same stomodaeum. Left: sections of gymnosperm (above) and angiosperm (below). Right: sections of gymnosperm (above) and fern (below) (100 X).

rowed along. This type of feeding often scored the xylem, or woody tissue, inward from the phloem (Fig. 2A). At times larvae girdled roots by removing the bark on nearly all sides (Fig. 2B), or in severe cases completely stripped the bark from roots leaving only stringers of xylem in the soil (Fig. 2C). Stomodaea of larvae that fed exclusively on bark of conifer roots appeared as shown in Figure 3A. Some larvae, instead of girdling roots or stripping bark, fed at right angles to roots and severed them (Fig. 2D).

After severing a root, some larvae began feeding on one end of the severed root, biting off lengths of root as they followed the root through the soil. In some cases, root segments were bitten off and ingested whole; in other cases, larvae stripped away the bark before ingesting xylem. Whether the stripping was done before or after the segment was bitten off is not known. Root segments from which the bark had been stripped were often intermingled with whole segments in the same larval gut (Fig. 4).

Some larvae severed root segments, stripped the bark from the woody tissue, and then split the xylem lengthwise into two or more fragments before ingesting it (Fig. 3B). Other larvae did not bite off whole root segments but chewed roots into fine pieces prior to ingestion. Ends of roots so eaten had a gnawed appearance (Figs. 2E and 3C).

Root fragments removed from the guts indicated that most larvae masticated roots before ingestion. Roughly only 30 percent of the larvae had bitten off and ingested whole root segments. Many larvae ate the phloem and outer bark before biting off a root segment. Even very small roots that could easily have been ingested intact were often stripped.

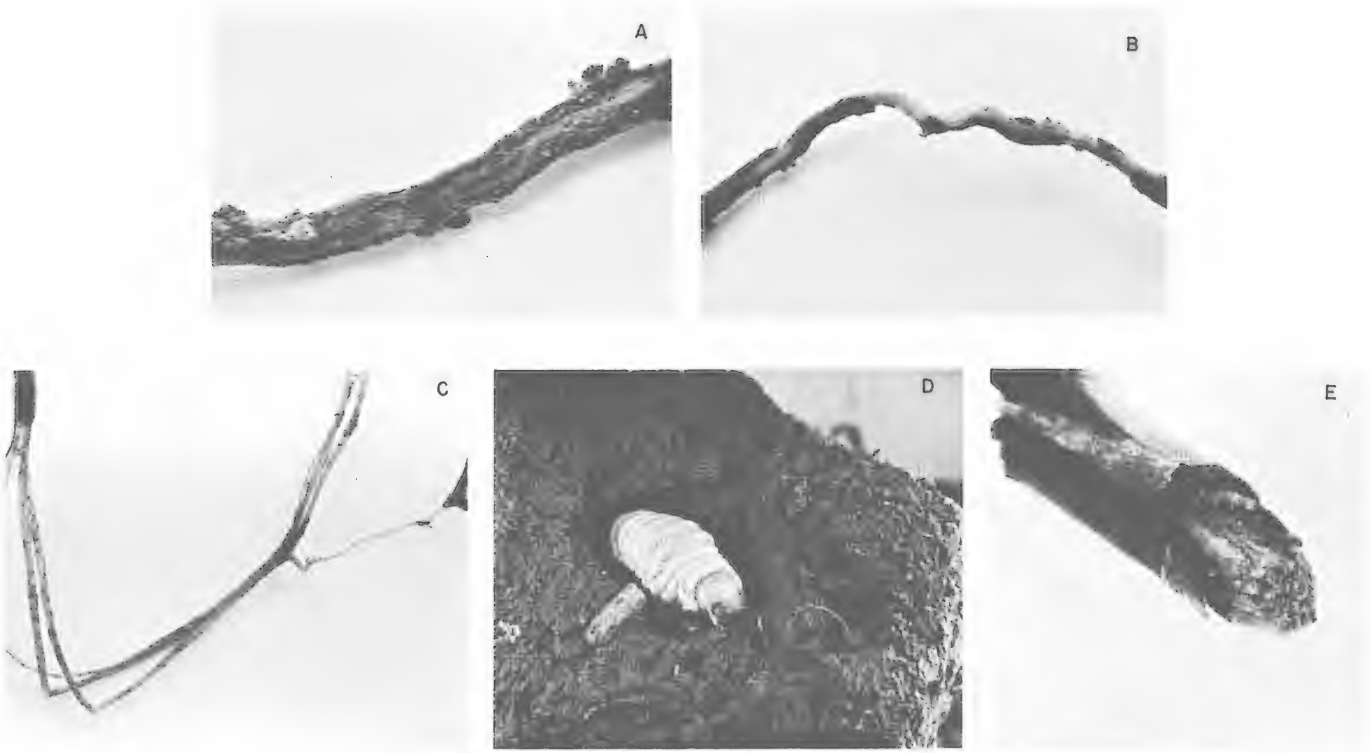


Figure 2. Damage to conifer roots by larvae of *Pleocoma*. A. Douglas-fir root damaged by small *P. simi* larva. Bark was eaten from one side of root while xylem tissue was only superficially scored. B. A third instar girdled this root by removing most of the bark. C. A larva completely stripped bark from this root leaving only stringers of xylem. Portions of root in upper left and upper right are undamaged. D. A small larva in its burrow with severed root. E. A large *P. carinata* larva gnawed end of root and ate away portion of upper surface (3 X).

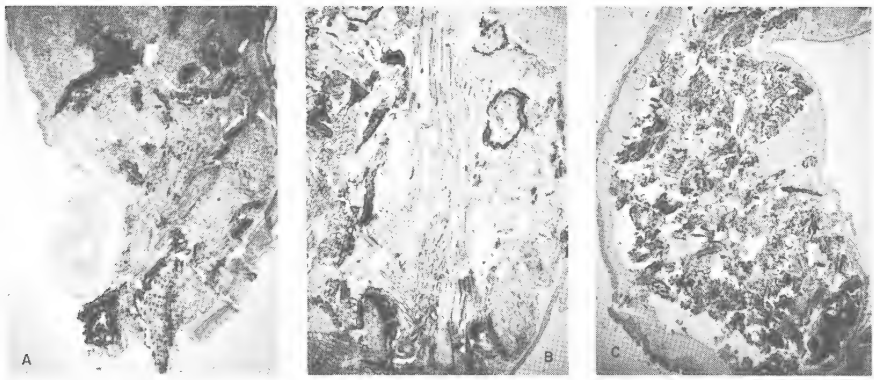


Figure 3. Photomicrographs of sagittal sections of *Pleocoma* larval stomodaea containing conifer roots illustrating three ways in which larvae feed on roots (all photos 22 X). A. Larva had fed only on bark of Douglas-fir root. Little or no xylem present in stomodaeum. B. Larva stripped bark from conifer root, masticated pieces of xylem, severed the xylem (seen lying vertically in left center of photo), then ingested everything. C. Larva had masticated entire Douglas-fir root into small pieces before ingestion.

Though root sizes available to larvae varied widely, most larvae appeared to avoid larger roots and restricted their feeding to smaller, more fibrous roots, generally less than 2 mm in diameter. As an example, a fifth instar *P. dubitalis*, when exhumed, had burrowed without feeding for at least 5 cm along a root 5 mm in diameter, but began feeding when it encountered a small branch root (Fig. 5). Two other unearthed larvae had burrowed through the soil paralleling roots 19 mm and 25 mm in diameter, respectively, without feeding on either of them. Generally, the larger the larva, the larger the whole root segments or root fragments found in the guts (Table 2). However, this is no indication that bigger larvae preferred larger roots or that smaller larvae preferred smaller roots. In a smaller larva, a smaller tentorium restricts expansion of the oesophagus, hence restricting the size of roots that can be eaten.

After having been chewed by the mandibles, root segments or root fragments showed little or no change in size as they passed through the alimentary system, because *Pleocoma* larvae have no special proventricular teeth, pads, or spines to further masticate roots (Areekul, 1957). Root fragments removed from proctodaea were the same size as those removed from respective stomodaea. Upon reaching the colon, food material is usually compacted before being excreted. However, relatively large chunks of xylem found in frass pellets collected in larval burrows or dissected from larval rectums showed no evidence of compaction (Fig. 6).

My observations indicate that larvae of the five species of *Pleocoma* studied in western Oregon feed very actively on roots as they burrow through the soil. Hovore (personal communication) notes that larvae of several species of *Pleocoma* in central California are also mobile feeders in the topsoil layers. However, he has observed that larvae of at least four species feeding on *Quercus* sp. or *Ceanothus* sp. in southern California seldom are found outside a clay hardpan layer. In this situation, unlike the central California species and most scarab larvae, Hovore (1971) reports that

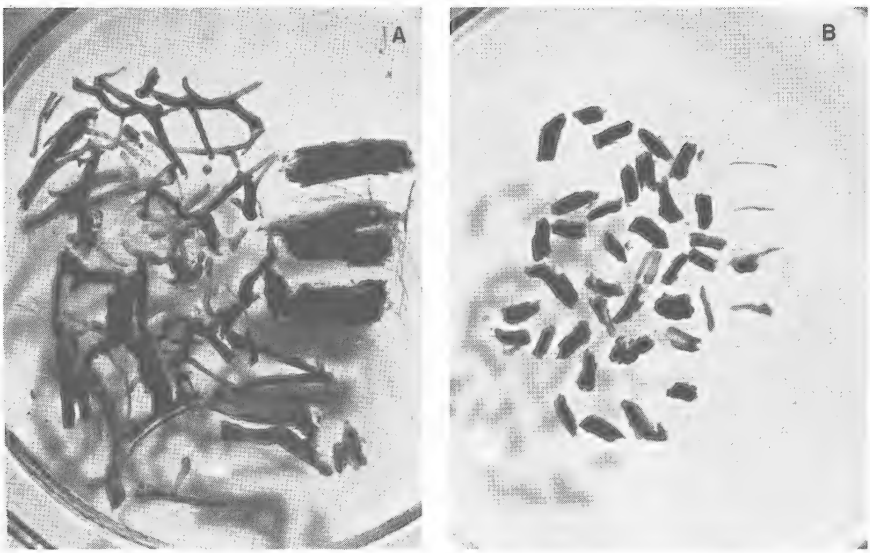


Figure 4. Segments of roots eaten by larvae as they followed roots through the soil. A. Roots from mesenteron of a large *P. carinata* larva. The three larger root segments on right side of photo have been ingested intact. Other roots in photo are segments of xylem from which bark has been stripped. B. Root segments slightly over 1 mm long eaten by second instar *P. simi* larva. Four roots on right side of photo have had bark stripped from them. Other root segments have been eaten intact (5 X).

TABLE 2. Size of roots found in the alimentary systems of *Pleocoma* larvae collected in coniferous forests of western Oregon.

Larvae		Average size (mm) of roots or root fragments ingested			
		Intact roots		Root fragments	
Instar or size	No. examined	Length	Width	Longest dimension	Narrowest dimension
		P. dubitalis			
2	34	1.03	0.46	0.91	0.42
3	18	1.46	.64	1.17	.49
4	10	1.71	.78	1.41	.60
5	12	1.85	.65	2.04	.83
6	19	2.35	.94	2.22	.84
7	17	2.82	1.02	2.92	1.07
8	9	2.00	1.10	2.93	1.07
9-	14	3.65	1.50	3.83	1.29
		P. simi			
small	33	1.17	.43	1.19	.47
medium	47	2.58	.84	2.29	.96
large	35	2.98	.77	3.30	1.31
		P. carinata			
small	7	1.15	.42	.92	.50
medium	9	2.38	1.11	2.24	1.01
large	11	3.91	.45	2.98	1.19

Figure 5. Fourth or fifth instar *P. dubitalis* in soil burrow. The larva had fed on a small Douglas-fir root (arrow) that it encountered after burrowing along a larger root (2 X).

these grubs appear to be sedentary feeders that enlarge their smooth, hardball burrows as their body size increases, and feed on rootlets that form "an enlarged tissue nodule at the point of larval feeding, assuring the larva of a constant food supply at the burrow."

Exuvia

At times the most abundant material in the guts of most larvae was the exuvia of the previous instar, that was consumed following ecdysis. Larvae usually consumed all of the cast skin, feeding first on the abdominal and thoracic portions. In some cases, the cast skin was so finely chewed that only setae were identifiable. In other cases, fairly large chunks of exuvia were found in the alimentary canal (Fig. 7). Even the cast mandibles were eaten—larvae severed them from the rest of the exuvia near the condyle and ingested them intact. All stages of larvae consumed their exuvia, except, of course, first instars which consumed the egg chorion. Several laboratory-reared second instars consumed their exuvia in 6 to 10 days after moulting.

Soil

Irregular particles of mineral soil were found in all stomodaea. Soil particles were easily seen in otherwise empty guts but were difficult to find in guts packed with

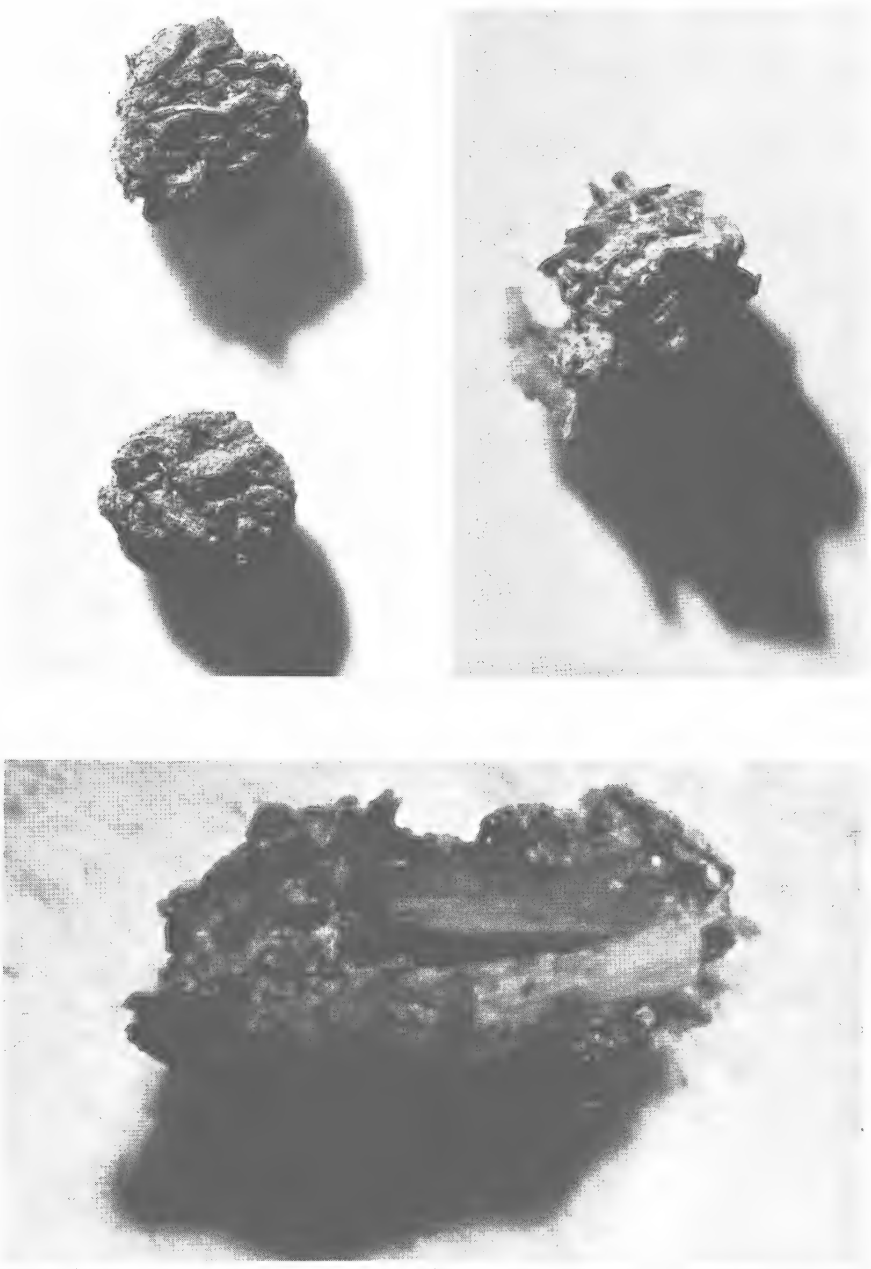


Figure 6. Frass of *Pleocoma* larvae. Upper left: two balls of compacted excrement composed of small pieces of root. Upper right: compact pellet composed entirely of exuvia. Setae can be seen protruding from left side of pellet. Below: pellet containing two large fragments of xylem which show no evidence of compaction (22 X).

roots or exuvia. Hence, I did not make a quantitative analysis of the amount of soil ingested. Smith and Hadley (1926) reported that guts of Japanese beetle larvae contained about 16 percent mineral matter by volume.

Other Material

A fine, fluffy, cotton-like, light-to-dark-brown material, tentatively identified as the remains of fungal hyphae, was interspersed throughout many stomodaea that were packed with roots or exuvia. It was sparse or absent in other root-packed stomodaea, yet completely filled some crops that were otherwise empty (Fig. 8). This material was found in larvae of all sizes and of each species in every month of the year; it is probably fairly abundant in the soil and could constitute a share of the larval diet, as indicated by Rivers (1890). There appears to be no relationship between these fungal hyphae remains and the hyphae forming the mantle on mycorrhizal rootlets that were eaten by *Pleocoma* larvae. However, six different species of mycorrhizal fungi, associated with mycorrhizal rootlets or mycorrhizal fragments, were identified in the guts of many larvae (Fig. 9).

During the moulting period, I often found what appeared to be mesenteron epithelium in the alimentary canal of many larvae. This material was most often found

Figure 7. Pieces of cast skin, from the previous instar, removed from the stomodaeum and ventriculus of a large *P. carinata* larva. The distal portion of an antenna lies in upper right center and at far left is the distal portion of a maxillary or labial palp (7 X).

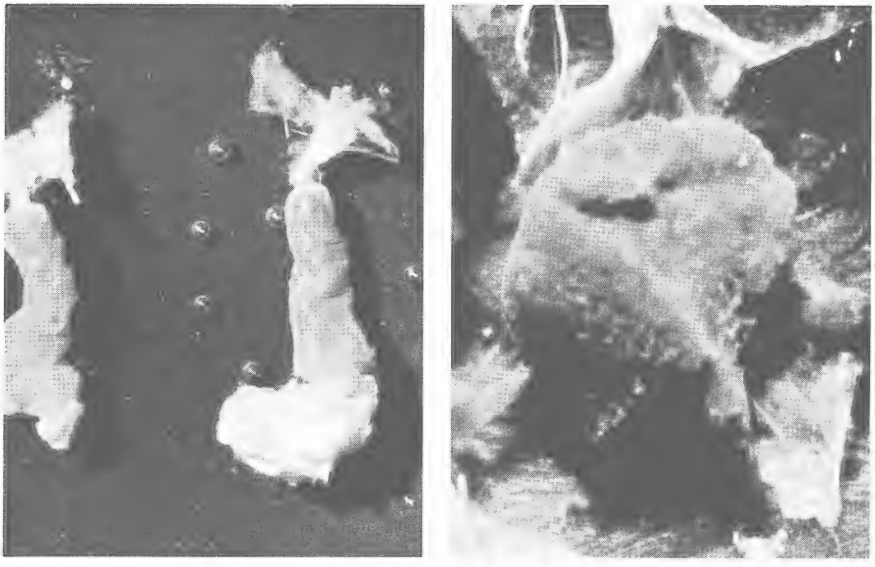


Figure 8. Material tentatively identified as remains of fungal hyphae. Left: two crops filled with the material (8 X). Right: a "wad" of material dissected from the oesophagus of a fifth instar (26 X).

in the mesenteron, less often in the proctodaeum, and never in the stomodaeum. Moreover, it occurred only in larval stages in which Areekul (1957) found degeneration of mesenteron epithelium in *Pleocoma.* According to Snodgrass (1935), there is probably more or less of a renovation of the stomach ventricular epithelium accompanying each larval moult in most holometabolous insects; in some cases the entire mesenteron epithelium becomes uniformly vacuolated and is cast off into the lumen (Day and Waterhouse, 1953).

Numerous small (about 1 mm in length), light-colored bodies, irregular in shape but always smooth-sided and usually flattened, were found throughout the year in the guts of many *Pleocoma* larvae. The bodies usually were seen in the mesenteron just beneath the peritrophic membrane where they completely enveloped the roots or other material (Fig. 10). When guts were empty, the bodies were scattered loosely in both the mesenteron and stomodaeum. One parasitologist, after studying the photograph in Figure 10, stated that, although they lacked classic form, the bodies resembled gregarine parasites.

Mites also were found occasionally in the digestive tracts of *Pleocoma* larvae. Though not identified, the mites resembled those found clustered in the integumental folds around the head capsules of many larvae.

Factors Influencing Feeding Habits

The amount and type of material eaten by larvae were closely related to the time of year when larvae were collected and the stages of larvae.

Figure 9. Photomicrograph of portion of stomodaeum showing fungus mantle (arrow) surrounding conifer rootlet. Hyphae of the mycorrhizal fungus *Cenococcum graniforme* (Sow.) Ferd. and Winge were detected in this stomodaeum (80 X).

Figure 10. Larval mesenteron showing irregularly shaped bodies, tentatively identified as gregarine parasites, lying just beneath the peritrophic membrane. Gut on right side of photo has been opened up to expose roots (8 X).

Time of Year

Most *P. dubitalis, P. simi*, and *P. carinata* larvae were actively feeding, and their alimentary systems were full of roots (Fig. 11B), from about mid-October until late June (Table 3). In early July, with the onset of physiological processes preceding moulting, larvae ceased feeding and their guts emptied (Fig. 11A). Alimentary systems remained empty until larvae moulted, after which they consumed their exuviae, usually in late August and September. Limited collections from the Hood River Valley indicated that the larval feeding behavior of *P. crinita* and *P. minor* is quite similar to that of the three species discussed above, with one exception: *Pleocoma minor* larvae ceased root-feeding in early June, an observation also reported by Ellertson and Ritcher (1959).

Stages of Larvae

Pleocoma larvae did not feed on roots during their first stage or during the early part of the second stage. First stage larvae, which do not leave the egg cells, fed on the egg chorion. Second stage larvae, after consuming their exuvia, began feeding on roots about mid-November shortly after moving away from the egg cells, and continued root feeding until the following June.

Areekul (1957) found that in late instar *Pleocoma* both sets of gastric caeca degenerate, accompanied by a shortening of the mesenteron and a lengthening of the stomodaea and proctodaea. These two conditions, plus the degeneration of the mesenteron epithelial cells, led Areekul to suggest that late instar *Pleocoma* cease feeding or change their feeding habits. My observations support his suggestion and, in fact, indicate that last instars pass the entire stadium without feeding. I found no roots

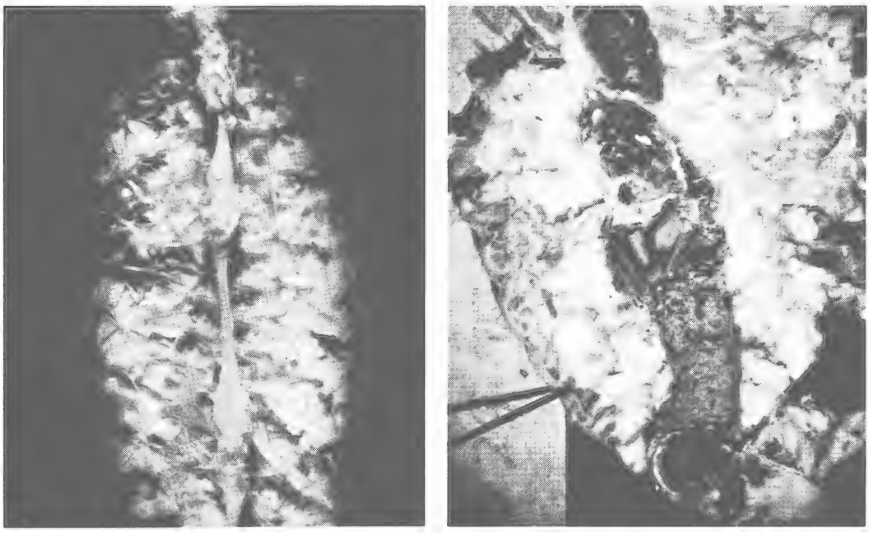


Figure 11. Alimentary canals of two *Pleocoma* larvae, empty (left), and full of conifer roots (right). The mid-ventriculus of the latter has been opened up to show large chunks of xylem tissue which had been eaten (2 X).

in the alimentary systems of 60 last instars collected at various times throughout the year, although some of these larvae had ingested and excreted exuvia of the penultimate instar.

A period of general inactivity accompanied the absence of feeding in the late instars. Most prepupal larvae spent the entire stadium in cells constructed less than 50 cm below the soil surface. Early in the stadium, the larvae wriggled about when removed from their cells, but prior to pupating they became lethargic. Two larvae that I inspected periodically were completely inactive for 41 and 72 days, respectively, before they pupated. There were indications that some larvae may become inactive as much as 6 months prior to pupating.

TABLE 3. Contents of the alimentary systems of 3 species of *Pleocoma* larvae collected in coniferous forests of western Oregon.

Date larvae collected	Contents of the alimentary system				
	Roots				
	Full	Partly Full	Trace	Exuvia	Empty
	(number of larvae)				
	P. dubitalis				
28 January	8				7
25 February	16				2
18 March	12	5			3
31 March	6				1
24 April	12		1		1
7 May	6				2
13 May	6	1			
29 May	12				2
28 June	4		1		2
8 July		1			6
28 July		1	6	1	6
15 August			3		2
25 August				1	5
13 September				5	2
21 October	8			2	4
21 November	9			3	1
22 December	12				1
	P. simi				
7 January	5				1
22 March	36	1	4		5
19 May	1				
26 May	30	1			1
16 June	18	2			1
19 July		2	1		1
16 August				1	
26 August			2	4	1
1 September			2	3	
14 October					3
7 December	5	6			5
	P. carinata				
3 January	4				1
28 March	3	2	1		1
11 May	1				
12 May	2				
21 May	12				
19 July		2	1		3
2 September				10	2
27 October	1				

Role of Pleocoma in the Forest

Although roots of coniferous trees were found to be the major component of the larval diet in old-growth forests in western Oregon, there are at least two reasons why *Pleocoma* larvae are probably not a serious problem in mature stands. First of all, *Pleocoma* larvae were not abundant; populations varied from 0 to 46 larvae per m^2 and averaged only 6 larvae per m^2 in more than 60 sample holes. This average is low compared to averages of 84 and 227 larvae per m^2 for *P. crinita* and *P. minor,* respectively, in Hood River Valley apple orchards (Ellertson and Ritcher, 1959). Feeding damage by such large populations of larvae resulted in the slow decline of apple and other pome fruit trees. Secondly, larvae generally fed only on small roots, generally those 2 mm or less in diameter. This contrasts with damage done by *Pleocoma* larvae in orchards where not only fibrous roots but main roots and even underground portions of the trunk were scored or destroyed by grubs (Ellertson and Ritcher, 1959). Another factor is that larvae are not feeding on roots for at least a two-month period from the first part of July to early September.

Pleocoma larvae are a potential pest of forest regeneration. This potential exists not only in forested areas that have been clearcut and are being regenerated by tiny seedlings, but also on denuded lands where forests are being established for the first time. Because *Pleocoma* larvae feed inconspicuously and unnoticed underground, they might be responsible for some of the seedling mortality that has been experienced in most reforestation programs. Whether young trees would be damaged or killed at any given area or time would depend on several factors, among which are: abundance and size of larvae, age and species of seedlings and extent of root system, type of feeding damage to roots, availability of other food (such as roots of shrubs), site and soil type, time of year of damage, and moisture and weather conditions.

In western Oregon, and elsewhere, as mature forests are cut and the land transformed to tree farms and extensive forest plantations, insects that caused relatively minor damage to the mature forest can be expected to flourish. In many areas both in this country and Canada, accelerated plantation and reforestation programs often have been accompanied by such serious insect problems that planting programs have been curtailed or in some cases abandoned. Because of the many difficulties involved in establishing new forests, any agent that interferes with growth of young trees is important.

Acknowledgements

I thank Professors Paul O. Ritcher and Julius A. Rudinsky, Department of Entomology, Oregon State University, for providing funds for this work, and for suggestions and criticisms during the study. Dr. Gene D. Amman, Intermountain Forest and Range Experiment Station, Ogden, Utah, critically reviewed the manuscript. Dr. M. F. Day, Commonwealth Scientific and Industrial Research Organization, Division of Entomology, Canberra, Australia; Dr. Robert G. Minn, Forest Entomology and Pathology Laboratory, Canada Department of Forestry, Victoria, British Columbia; and Dr. James M. Trappe, Pacific Northwest Forest and Range Experiment Station, USDA Forest Service, Portland, Oregon, identified some of the material found in the larvae.

Literature Cited

Areekul, S. 1957. The comparative internal larval anatomy of several genera of Scarabaeidae (Coleoptera). Ann. Entomol. Soc. Amer. 50(6): 562-577.

Day, M. F., and D. F. Waterhouse. 1953. Structure of the alimentary system. *In*: Insect Physiology, ed. Kenneth D. Roeder. New York, Wiley, p. 273-298.
Ellertson, F. E. 1956. *Pleocoma oregonensis* Leach as a pest in sweet cherry orchards. J. Econ. Entomol. 49(3): 431.
————, and P. O. Ritcher. 1959. Biology of Rain Beetles, *Pleocoma* spp., Associated with Fruit Trees in Wasco and Hood River Counties. Corvallis, Oreg. Agric. Exp. Stn. Tech. Bull. 44, 42 p.
Hazeltine, W. 1950. Observations on flights of *Pleocoma conjungens.* Pan-Pac. Entomol. 26(4): 188-189.
————. 1952. Notes on flights and food plants of *Pleocoma.* Pan-Pac. Entomol. 28(4): 202.
Hovore, F. T. 1971. A new *Pleocoma* from southern California with notes on additional species (Coleoptera:Scarabaeidae). Pan-Pac. Entomol. 47(3): 193-201.
Linsley, E. G. 1938. Notes on the habits, distribution, and status of some species of *Pleocoma.* Pan-Pac. Entomol. 14(2): 49-58.
————. 1945. Further notes on some species of *Pleocoma.* Pan-Pac. Entomol. 21(3): 110-114.
————. 1957. Distributional records for some species of *Pleocoma.* Pan-Pac. Entomol. 33(2): 102-104.
Ritcher, P. O., and V. Olney. 1953. White grubs as apple tree pests in the Hood River Valley. Oreg. State Hortic. Soc. Proc. 45: 41-42.
————, and F. M. Beer. 1956. Notes on the biology of *Pleocoma dubitalis dubitalis* Davis (Coleoptera:Scarabaeidae). Pan-Pac. Entomol. 37(4): 181-184.
Rivers, J. J. 1890. Habits in the life history of *Pleocoma behrensii* Lec. Zoe 1: 24-26.
Smith, L. B., and C. H. Hadley. 1926. The Japanese Beetle. Washington, U.S. Govt. Print. Off., USDA Circ. 363. 66 p.
Snodgrass, R. E. 1935. Principles of Insect Morphology. New York, McGraw-Hill. 667 p.
Stein, W. I. 1963. *Pleocoma* larvae root feeders in western forests. Northwest Sci. 37(4): 126-143.

Received December 9, 1974.
Accepted for publication January 22, 1975.

L. Fraser Rasmussen[1]
and
Don C. Williams[2]

Department of Biology
Western Washington State College
Bellingham, Washington

The Occurrence and Distribution of Mercury in Marine Organisms in Bellingham Bay

Abstract

A survey of mercury levels in intertidal organisms collected from several sites in Bellingham Bay indicated that those organisms contained one order of magnitude more mercury than organisms taken from Birch Bay (0.15 vs. 0.015 mg Hg/kg), an area free of industrial mercury pollution. Dungeness crabs taken from Bellingham Bay contained generally three to four times as much mercury as those from Samish Bay. The mean mercury concentration in the antennal gland of this organism (the organ with the highest mercury concentration) was 0.6 mg Hg/kg.

Introduction

It has become apparent in the last several years that substantial amounts of mercury have been released into the environment through various industrial processes and that certain organisms within these affected areas accumulate this mercury in various forms (Westöö, 1966, 1967; Jensen and Jernelöv, 1969). Bellingham Bay, on Puget Sound, represents an excellent area for the study of mercury accumulation in organisms as Georgia-Pacific Corporation maintains a chlor-alkali facility that for a number of years has released mercury-contaminated effluent into the bay.

The facility uses a continuous-flow mercury cathode cell to produce chlorine gas and caustic soda. Figures for 1968 indicate that 23.1 percent of mercury used in the United States was for the production of these two products (D'Itri, 1972). Furthermore, until 1970 this industry, by releasing untreated effluent, was the largest contributor of mercury to aquatic environments. Bellingham Bay has been contaminated with mercury effluent in quantities of 10 to 15 lbs per day from 1965 to 1970. Presents levels entering the bay are 0.25 to 0.5 lbs per day as a result of controls requiring reclamation of mercury from the effluent.

Once sedimented with organic materials, mercury remains in the aquatic environment either in the bottom sediments or accumulates in various organisms. Mercury may thus present a potential toxicological problem for a number of years.

A 1971 analysis of sediments in Bellingham Bay revealed high (6,900 μg/kg mean) and homogeneous levels of mercury in the top 5 cm of the sediment throughout much of the bay (Bothner and Piper, 1973). Although Bellingham Bay has experienced extensive mercury pollution, there have been only minimal efforts to determine mercury levels in the organisms exposed to the heavy metal. Periodic analysis of the intertidal and subtidal organisms exposed to unnaturally high mercury

[1] Department of Fisheries and Wildlife, Oregon State University, Marine Science Center, Newport, Oregon 96325.
[2] To whom requests for reprints should be made.

levels should be conducted in order to determine the degree of turnover in this marine environment. For these reasons it was deemed essential to conduct a survey of organisms in the bay and to compare them to organisms collected from an area removed from mercury pollution, such as Birch Bay.

Materials and Methods

Marine organisms in Bellingham Bay and surrounding area were tested for mercury content from March to May, 1973. In addition, the Dungeness crab, *C. magister,* a subtidal species, was collected from several sites in Bellingham and Samish Bays, and specific tissues were examined for mercury concentration. Intertidal organisms were collected from a number of sites, as designated in Figure 1. The greatest number of organisms from Bellingham Bay itself were taken from Post Point (Station 2) and north Bellingham Bay beaches (Stations 4 and 5). These two areas represent, respectively, the nearest southern and northern points to the Georgia-Pacific Corporation that possess a multiplicity of marine organisms. The geographical limits within which organisms were collected were Birch Bay on the north and Samish Bay on the south. The Birch Bay area was selected for a control site, being the farthest away from sources of industrial or natural mercury pollution.

Species representing five phyla of invertebrates (Coelenterates, Annelids, Arthropods, Molluscs, and Echinoderms) and one class of fishes (Pisces) were collected at periods of low tide. Muscular tissue was sliced into small pieces with a razor blade and excess moisture removed by placing on absorbent paper. Visceral tissue was placed on the absorbent paper without further preparation. None of the tissue analyzed required homogenization to effect complete digestion. Any tissue not assayed within a 24-hour period after removal from the animal was stored in glass vials and frozen at -15°C. Whenever organisms were of larger size, specific organs or sections of tissue were assayed separately in order to assess the differential accumulation of mercury in tissue. All samples were analyzed for total mercury content by the wet digestion pressure method of Adrian (1971). Tissue was excised from the specimens and placed on an absorbent, high-grade paper to remove any exogenous water. One to four grams of tissue was weighed into 4 oz. Nalgene bottles, and 3.0 ml 70-72 percent perchloric acid and 7.0 ml concentrated nitric acid were added to the bottles. The vessels were capped and allowed to stand at room temperature overnight to predigest. The digestion was completed by heating the samples in a 60°C shaking water bath for 1-2 hours, after which they were cooled and diluted to 15 ml with distilled, deionized water. All samples were assayed by a modification of the Pekin-Elmer stannous chloride reduction method using a Perkin-Elmer Model 306 Atomic Absorption Spectrophotometer.

Results and Discussion

Table 1 indicates the mercury levels found in the tissues of organisms representing five phyla of marine invertebrates, two species of intertidal fish, and four species of marine algae. Molluscs, the most abundant group in the areas surveyed, composed the largest percentage of organisms analyzed. The Dungeness crab, *Cancer magister,* the only subtidal species analyzed, is presented separately in Table 2.

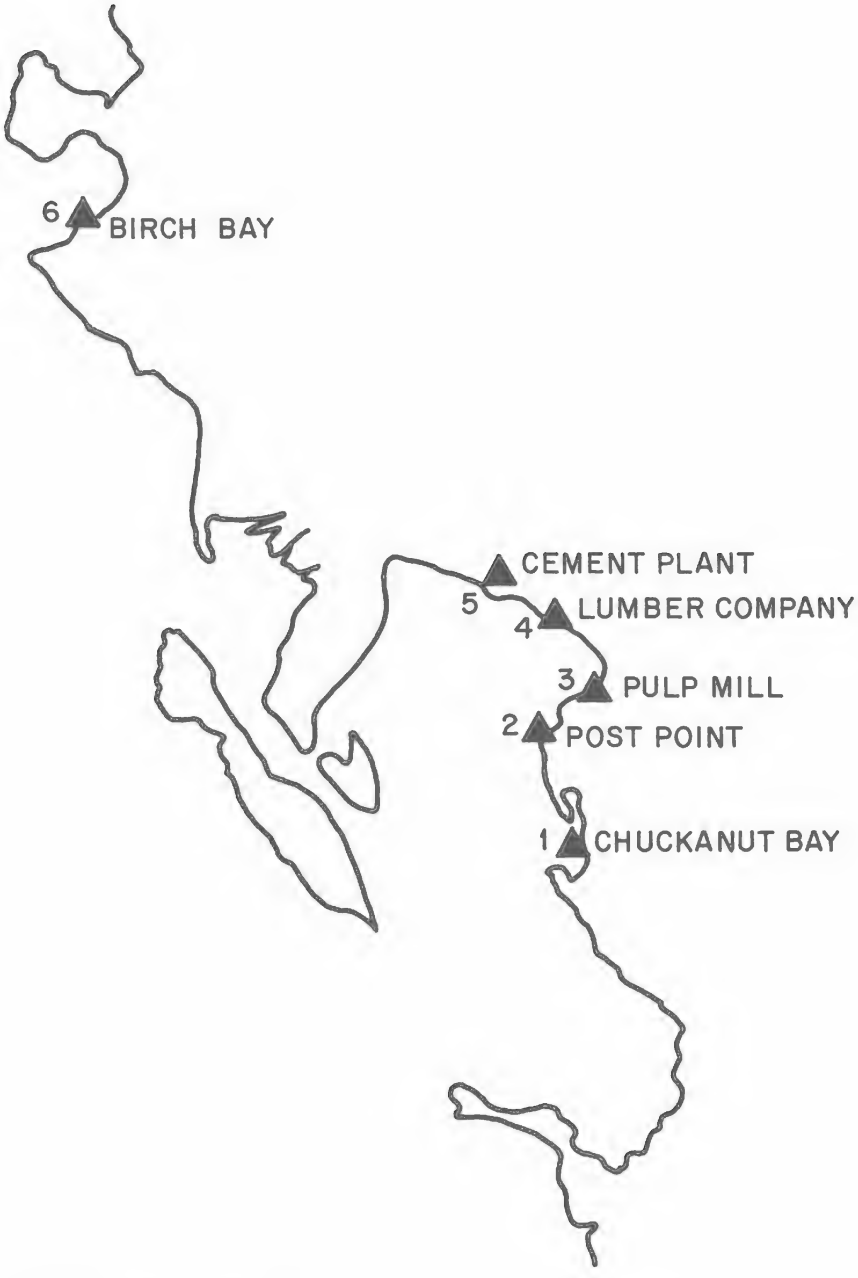


Figure 1. Collection sites for organisms analyzed for mercury concentrations.

TABLE 1. A survey of mercury content in intertidal species from Bellingham Bay and vicinity. Number of organisms analyzed indicated in parentheses. Values are means ± standard error where indicated.

Collection* site (Station #)	Organism	Tissue sample	Total Hg mg/kg wet weight
	MOLLUSCS		
1	Soft shell clam, *Mya arenaria* (6)	siphon	0.16 ± .006
		viscera	0.10 ± .009
1	Butter clam, *Saxidomus giganteus* (2)	siphon	0.02 ± .001
		viscera	0.06 ± .013
1	Edible mussel, *Mytilus edulis* (10)	whole animal (w.a.)	0.12 ± .020
2	Steamer clam, *Prototheaca staminea* (13)	siphon	0.17 ± .008
		viscera	0.13 ± .008
2	Butter clam, *Saxidomus giganteus* (4)	siphon	0.05 ± .001
		viscera & foot	0.27 ± .080
2	Cockle, *Clinocardium nuttallii* (5)	viscera	0.08 ± .010
2	Bent nose clam, *Macoma nasuta* (2)	siphon	0.11 ± .001
		viscera	0.09 ± .0004
2	Edible mussel, *Mytilus edulis* (17)	w.a.	0.12 ± .003
2	Limpet, *Acmea persona* (3)	w.a.	0.12 ± .020
2	Wrinkled thais, *Thais lamellosa* (2)	w.a.	0.12 ± .020
2	Sea lemon, *Anisodoris nobilis* (1)	viscera	0.30
2	Ringed nudibranch, *Diaulula sandiegensis* (5)	viscera	0.09 ± .030
2	Pacific oyster, *Crassostrea gigas* (2)	w.a.	0.10 ± .02
4	Edible mussel, *Mytilus edulis* (15)	w.a.	0.05 ± .001
5	Edible mussel, *Mytilus edulis* (14)	w.a.	0.05 ± .002
6	Edible mussel, *Mytilus edulis* (5)	w.a.	0.01 ± .0006
6	Butter clam, *Saxidomus giganteus* (8)	siphon	0.01 ± .001
		viscera	0.02 ± .0008
6	Steamer clam, *Prototheaca staminea* (3)	siphon	0.01 ± .001
		viscera	0.02 ± .0008
6	Horse clam, *Schizothaerus nuttallii* (10)	siphon	0.01 ± .001
		viscera & foot	0.01 ± .002
6	Bent nose clam, *Macoma nasuta* (3)	w.a.	0.02 ± .001
	ARTHROPODS		
2	Purple shore crab, *Hemigrapsus nudus* (16)	gill	0.17 ± .002
		hepatopancreas	0.26 ± .012
2	Hairy shore crab, *Hemigrapsus oregonensis* (4)	gill	0.20 ± .109
		hepatopancreas	0.13 ± .001
2	Red Cancer crab, *Cancer productus* (5)	gill, hepat., & muscle	0.16 ± .038
3	Hairy shore crab, *Hemigrapsus oregonensis* (6)	gill & hepat.	0.16 ± .023
4	Hairy shore crab, *Hemigrapsus oregonensis* (10)	gill & hepat.	0.07 ± .003
5	Hairy shore crab, *Hemigrapsus oregonensis* (8)	gill & hepat.	0.07 ± .005
	ANNELIDS		
1	Nephtys spp. (2)	w.a.	0.05 ± .005
1	Pile worm, *Nereis procera* (2)	w.a.	0.02 ± .001

(Continued overleaf)

TABLE 1. (continued)

Collection* site (Station #)	Organism	Tissue sample	Total Hg mg/kg wet weight
2	Pile worm, *Nereis procera* (6)	w.a.	0.04 ± .009
2	Mussel worm, *Nereis vexillosa* (3)	w.a.	0.06 ± .057
4	Pile worm, *Nereis procera* (1)	w.a.	0.06
4	Mussel worm, *Nereis vexillosa* (1)	w.a.	0.09
6	Pile worm, *Nereis procera* (3)	w.a.	0.02 ± .006
	ECHINODERMS		
2	Mottled star, *Evasterias troschelii* (1)	stomach & caeca	0.09
2	Purple star, *Pisaster ochraceus* (2)	stomach & caeca	0.24 ± .003
	COELENTERATES		
2	Burrowing anemone, *Anthopleura artemisia* (3)	muscle & viscera	0.06 ± .006
	INTERTIDAL FISH		
2	Blennie, *Anoplarchus* spp. (3)	muscle	0.08 ± .03
2	Tidepool sculpin, *Oligocottus maculosus* (3)	muscle	0.24 ± .11
	ALGAE		
2	*Ulva lactuca* (2)	———	0.05
2	*Iridaea chordate* (1)	———	0.06
2	*Fucus gardneri* (1)	———	0.04
4	*Ulva lactuca* (1)	———	0.03

*Station numbers correspond to the following locations: (1) Chuckanut Bay; (2) Post Point; (3) Pulp Mill; (4) Lumber Company; (5) Cement Plant; (6) Birch Bay. See Figure 1 for a visual description of collection sites.

TABLE 2. Distribution of total mercury in tissues of *Cancer magister* collected from Bellingham Bay and Samish Bay. Values are means ± standard error; number of samples given in parentheses.

Tissue		Total Hg mg/kg wet weight
	Bellingham Bay	
Antennal gland	(7)	0.60 ± .092[a]
Hepatopancreas	(7)	0.41 ± .049[a]
Gill	(8)	0.27 ± .036[b]
Muscle	(8)	0.23 ± .045[a]
Heart	(7)	0.19 ± .014
	Samish Bay	
Antennal gland	(6)	0.25 ± .051
Hepatopancreas	(6)	0.19 ± .047
Gill	(8)	0.15 ± .029
Heart	(6)	0.13 ± .029
Muscle	(6)	0.05 ± .014

[a] Significantly higher in Hg conc. than Samish Bay crabs at the 1 percent level.
[b] Significantly higher in Hg conc. than Samish Bay crabs at the 5 percent level.

Mercury concentration in the tissues of all intertidal organisms within the confines of Bellingham Bay (Stations 2, 3, 4 and 5) ranged from 0.04 to 0.30 mg Hg/kg wet weight (Table 1). Results indicated that organisms collected from Post Point area tended to have a slightly higher concentration of mercury than those sampled immediately south of the Georgia-Pacific chlor-alkali facility, a source of mercury pollution. Shore crabs (*Hemigrapsus oregonensis*) from Station 3, a small beach within several hundred yards of the Georgia-Pacific chlor-alkali facility, had a mean concentration of 0.16 mg Hg/kg, which was no higher than levels in the same species collected from Post Point (Station 2). No single group of intertidal organisms taken from Bellingham Bay displayed higher mercury levels than another group; however, annelid worms appeared to be uniformly lower in mercury than any other group. In the organisms in which specific tissues were analyzed there was no definable pattern of one tissue accumulating more mercury than another. Organisms taken from the control site, Birch Bay (Station 6), were generally one order of magnitude lower than Bellingham Bay species, which indicates that industrial mercury effluent has increased levels within these organisms beyond natural background concentrations. In a very limited study in May 1970, just prior to instituting controls on chlor-alkali mercury effluent, the Washington State Department of Ecology (1971) reported that mercury levels in Bellingham Bay mussels (*Mytilus edulis*) were approximately 0.25 mg Hg/kg, a value twice that determined in the present study.

Mercury levels in *C. magister* collected from Bellingham Bay were found to be significantly higher than those collected from Samish Bay, the control site (Table 2). The edible portion of the crab (muscle) was 4.5 times higher in mercury concentration in Bellingham Bay than in neighboring Samish Bay (0.23 vs. 0.05 mg Hg/kg). It is reasonable that mercury levels would be higher in this subtidal organism than in those surveyed in the intertidal region. *Cancer magister,* known as a rather transient organism, would come in contact with sediments of higher mercury concentration than would intertidal species. In addition, *C. magister* feeds on a higher trophic level than the other invertebrates analyzed and thus would accumulate more mercury through the food chain.

The dynamics of mercury ecology and cycling in aquatic environments have recently been reviewed by Fagerstrom and Jernelöv (1972) and Gavis and Ferguson (1972). Several points of interest with respect to the local environmental mercury problem should be elucidated. Although mercury levels in the present survey of intertidal organisms are within the safety standards established by the Food and Drug Administration (0.5 mg Hg/kg, designated as the safety limit on foodstuffs for human consumption), it should not be concluded that a mercury pollution problem does not exist.

The availability of mercury to organisms in an aquatic system is dependent on a number of complex physical, chemical, and biological considerations, of which only a few of the more important will be mentioned. Unstable organic mercurials, such as the phenyl compounds, or mercury released as the inorganic divalent mercuric ion (Hg^{++}) are usually sedimented in particulate form after reacting with suspended organic matter. If these sediments are rich in microbiotic flora, the mercurials are readily transformed to monomethyl or dimethylmercury as a mechanism of detoxification by a number of bacterial or fungal organisms (Wood *et al.*, 1968; Landner,

1971; Jensen and Jernelöv, 1969). This biotransformation can take place in both aerobic and anaerobic sediments; however, turn-over is impeded in an anaerobic system in which much of the mercury is presented as insoluble HgS (Fagerstrom and Jernelöv, 1972). Much of the mercury entering Bellingham Bay might be expected to exist in such an insoluble form as a result of combining with spent sulfite liquor effluent from Georgia-Pacific's calcium sulfite pulping process. Its insolubility would essentially trap mercury in a slowly reactive form that might remain in the aquatic sediment as a potential pollutant for a number of years. Basing his findings on a laboratory experiment, Jernelöv (1970) has estimated that mercury could continue to be available from the sediment of several Swedish lakes for 10 to 100 years.

Possible evidence for an aerobic system can be cited from a 1971 study of mercury content in the sediments of Bellingham Bay. This study determined that mercury levels were nearly 18 mg Hg/kg in close proximity to the chlor-alkali plant and 5 mg Hg/kg 3.5 miles away from the effluent source (Bothner and Piper, 1973). Further, it was reported in this study that sediments were uniform in mercury content within the top 5 cm, indicative of macro- and microbiotic activity and/or strong tidal currents. If sediment turnover is characteristic of the aquatic habitat, then an aerobic environment may predominate in which biological methylation of inorganic mercury would take place more rapidly. In addition, the rate of methylation has been found to be positively correlated with the degree of microbiological activity, which, in turn, is partially governed by the degree of temperature fluctuation (Fagerstrom and Jernelöv, 1972; Uthe *et al.,* 1973). Vertical temperature-fluctuations in the upper ten meters of the water column measured in the area from Georgia-Pacific Corporation to Post Point during 1959 and 1960 revealed a variation in temperature, ranging from 9.7°C in November to 17.0°C in July (Collias *et al.,* 1966). During the period of higher temperatures, methylation rates most likely increase within this area of the bay. In conjunction with a potential increase in the metabolic rates of higher organisms present, there may exist an amplification of the amount of mercury taken up by these organisms.

It is known that monomethylmercury (CH_3Hg^+) is more available to react with the tissue of organisms than dimethylmercury (CH_3HgCH_3). The latter mercurial is sensitive to degradation by u.v. light and does not have the capacity to react with sulfhydryl groups as does CH_3Hg^+ (Gavis and Ferguson, 1972). It is thought that CH_3HgCH_3 dissociates to CH_3Hg^+ within the cell (Webb, 1966). Which of these two forms exists in an aquatic system is largely dependent on the pH of the sediments and surrounding water. At pH 7.0 and below, CH_3Hg^+ is the predominant species; however, above pH 7.8, CH_3HgCH_3 will predominate (Fagerstrom and Jernelöv, 1972). Measurements of pH of water from each of the sampling stations ranged from 6.7 to 6.9, the range within which CH_3Hg^+ would be most prevalent. No information has been located on pH values of Bellingham Bay sediments.

Although it was not feasible to analyze for specific mercurials in the present investigation, there is abundant evidence that mercury within aquatic organisms is present as the more toxic CH_3Hg^+ (Gavis and Ferguson, 1972; Lockhart *et al.,* 1972). Estimates of the CH_3Hg^+ content in contaminated marine and freshwater fish have been found to range from 82 to 92 percent respectively, depending on the organ or tissue analyzed (Zitko *et al.,* 1971).

Literature Cited

Adrian, W. J. 1971. A new wet digestion method for biological material utilizing pressure. Atomic Absorption Newsletter 10(4): 96.

Bothner, M. H., and D. Z. Piper. 1973. The distribution of mercury in sediment cores from Bellingham Bay, Washington. *In* D. R. Buhler (ed.), Proceedings of the Workshop on Mercury in the Environment. Oregon State Univ. Press, Corvallis, Oregon.

Collias, E. E., C. A. Barnes, C. B. Murty, and D. V. Hansen. 1966. An Oceanographic Survey of the Bellingham-Samish System. Vol. II. Univ. of Wash. Dept. of Oceanography.

D'Itri, F. M. 1972. The Environmental Mercury Problem. CRC Press, Cleveland, Ohio. p. 43.

Fagerstrom, J., and A. Jernelöv. 1972. Some aspects of the quantitative ecology of mercury. Water Research 6: 1193-1202.

Gavis, J., and J. F. Ferguson. 1972. The cycling of mercury through the environment. Water Research 6: 989-1008.

Jensen, S., and A. Jernelöv. 1969. Biological methylation of mercury in aquatic organisms. Nature 223: 753-754.

Jernelöv, A. 1970. Release of methyl mercury from sediments with layers containing inorganic mercury at different depths. Limnol. Oceanogr. 15: 958-960.

Landner, L. 1971. Biochemical model for the biological methylation of mercury suggested from methylation studies in vivo with *Neurospora crassa.* Nature 230: 452-453.

Lockhart, W. L., J. F. Uthe, A. R. Kenney, and P. M. Mehrle. 1972. Methylmercury in northern pike (*Esox lucius*): Distribution, elimination, and some biochemical characteristics of contaminated fish. J. Fish. Res. Bd. Canada 29: 1519-1523.

Uthe, J. F., F. M. Atton, and L. M. Royer. 1973. Uptake of mercury by caged rainbow trout (*Salmo gairdneri*) in the South Saskatchewan River. J. Fish. Res. Bd. Canada 30: 643-650.

Washington State Department of Ecology. 1971. Mercury in Washington State. Bulletin.

Webb, J. L. 1966. Mercurials. *In* Enzyme and Metabolic Inhibitors. Vol. II. Academic Press, New York. p. 729-985.

Westöö, G. 1966. Determination of methylmercury compounds in foodstuffs. I. Methylmercury compounds in fish, identification and determination. Acta Chem. Scand. 20: 2131-2137.

————. 1967. Determination of methylmercury compounds in foodstuffs. II. Determination of methylmercury in fish, egg, meat and liver. Acta Chem. Scand. 21: 1790-1800.

Wood, J. M., F. S. Kennedy, and C. G. Rosen. 1968. Synthesis of methylmercury compounds by extracts of methanogenic bacterium. Nature 220: 173-174.

Zitko, V., B. J. Finlayson, D. J. Wildfish, J. M. Anderson, and A. C. Kohler. 1971. Methylmercury in freshwater and marine fishes in New Brunswick, in the Bay of Fundy, and on the Nova Scotia Banks. J. Fish. Res. Bd. Canada 28: 1285-1291.

Received July 23, 1974.
Accepted for publication January 2, 1975.

Nedavia Bethlahmy

USDA Forest Service
Intermountain Forest and Range Experiment Station[1]
Ogden, Utah

A Colorado Episode: Beetle Epidemic, Ghost Forests, More Streamflow[2]

Abstract

When a small watershed is clearcut, it temporarily yields more water. The implication is that water yield and land use are closely related. This interdependence is illustrated for two large watersheds in Colorado where bark beetles destroyed the living timber trees. Substantially greater water yields are still evident 25 years after the epidemic because significant elements of the watersheds have not yet reverted to their former status—dead trees still occupy the land, and have not yet been replaced by live trees. The variable hydrologic effects of the epidemic in the studied watersheds reflect differences in their exposures.

Introduction

Many experiments have shown that a small, forested watershed will yield more water after it is clearcut. This increase is temporary if a new forest becomes established, or may be permanent if a new land use is instituted. In a larger sense, the experiments demonstrate the principle that water yield is related to land use. Our knowledge of water yield as related to land use is based on experiments generally conducted on small watersheds of a few acres (cf. Hibbert, 1967). But we now have data to show that the principle holds true on areas covering hundreds of square miles.

Great winds have always affected man and his environment. Ages ago winds deposited the loess that covers vast areas in Europe, Asia, and North America (Robinson, 1951). In our own time, violent winds blew down forests in New England (Patric, 1974) and leveled swaths of giant trees in the forests of the Northwest. An intense wind that struck the high plateaus of Colorado in 1939 is of particular interest, not because it was unique, but because of events that followed in its wake: in the uprooted and weakened trees of the White River watershed, bark beetles multiplied to epidemic proportions and by 1946 had attacked and killed forest trees covering hundreds of square miles in both the White and Yampa River watersheds and eastward to the Continental Divide (Wygant and Nelson, 1949). When the epidemic finally ran its course, it covered 30 percent of the gaged watersheds and killed up to 80 percent of the forest trees.

Ecologic effects of the epidemic are visible and clearly evident. Before the epidemic the forests consisted primarily of Engelmann spruce and subalpine fir in a 4:1 ratio,[3] with basal area of 34 m^2/ha, and volume of 343 m^3/ha. Twenty-five years after

[1] Stationed in Moscow, Idaho, at the Forestry Sciences Laboratory, maintained in cooperation with University of Idaho.
[2] Paper presented at the 47th Annual Meeting of the Northwest Scientific Association at the University of British Columbia in Vancouver, B.C., on May 9, 1974.
[3] Silvicultural data furnished by Messrs. Ski Milanowski, U.S. Forest Service, Steamboat Springs, Colorado, and Donn B. Cahill, U.S. Forest Service, Denver, Colorado.

the epidemic, dead trees are still standing; new, live trees are again spruce and fir but in a 1:4 ratio; and basal area and volume are only 10 m^2/ha and 60 m^3/ha.

The beetle epidemic also changed the hydrology of the region, as evidenced when the data are subjected to specialized analytical techniques. Love (1955) was the first to suggest that streamflow increased after the beetles destroyed the timber on the White River watershed. He hypothesized a 2-inch (5.08 cm) yearly increase by analyzing limited streamflow and snow course data for both the White and the unaffected Elk River watersheds. Others (Bue *et al.*, 1955) objected to the analysis, contending that without further data it was not possible to prove whether streamflow increased in one watershed or decreased in the other.

This paper verifies Love's conclusions by offering additional data and subjecting them to rigorous analyses. Locations of the four studied watersheds[4] are shown in Figure 1. Yampa and White watersheds were affected by the epidemic, but Plateau and Elk watersheds were spared.

Analysis of Vertex Angles for Annual Water Yields

The following analysis of streamflow data uses a previously unreported "integrating triangle method" devised by the author to evaluate the response of watersheds to natural disturbances and management practices in the absence of long-term records. Complete documentation and review of the technique is currently underway, hence rigorous evaluation, in a statistical sense, has yet to be accomplished.

Consider a triangle having sides (a,b,c) that represent annual streamflow of the Elk, White, and Yampa watersheds (Fig. 2). The length of each side (L_s) represents a river's annual flow (x_i) expressed in terms of its pre-epidemic average (x_a).[5] If side a is the triangle's base and represents the Elk River's streamflow, then the opposed vertex angle A is readily calculated,[6] and may be used to characterize the relationship among the three watersheds. A significant change in their relationship would be reflected in the size of the vertex angle. Thus, if the epidemic induced increased streamflow of the White and Yampa rivers, then angle A should be smaller than its characteristic value prior to the epidemic.

The analysis showed that the average value of angle A decreased from 1.047 radians before the epidemic[7] to 0.987 radian after the epidemic. The change is significant at the 99 percent level of significance using student's "t" test.

A similar analysis using Plateau Creek as the triangle's base revealed that angle A decreased from a pre-epidemic value of 1.045 radians to 0.923 radian, and again, the change is highly significant at the 99 percent level of significance using student's "t" test.

Average values of vertex angle A for different periods are listed in Table 1.

---

[4] Identification numbers and areas of the four watersheds are: Elk at Clark (9.304, 534 km^2); Plateau near Colbran (9.965, 208 km^2); Yampa at Steamboat Springs (9.2395, 1564 km^2); White near Meeker (9.3045, 1974 km^2). Analyses are based on data in USGS Water Supply Papers 1313, 1733, 1924, 1925.

[5] $L_s = \arctan e^w$, where $w = (x_i - x_a)/(2x_a)$.

[6] $A = \arcsin \dfrac{2\sqrt{s(s-a)(s-b)(s-c)}}{bc}$ and $s = \dfrac{a+b+c}{2}$.

[7] The years 1930-1940 comprise the pre-epidemic period; 1946-1965 the postepidemic period. In other analyses the pre-epidemic period is 1911-1940.

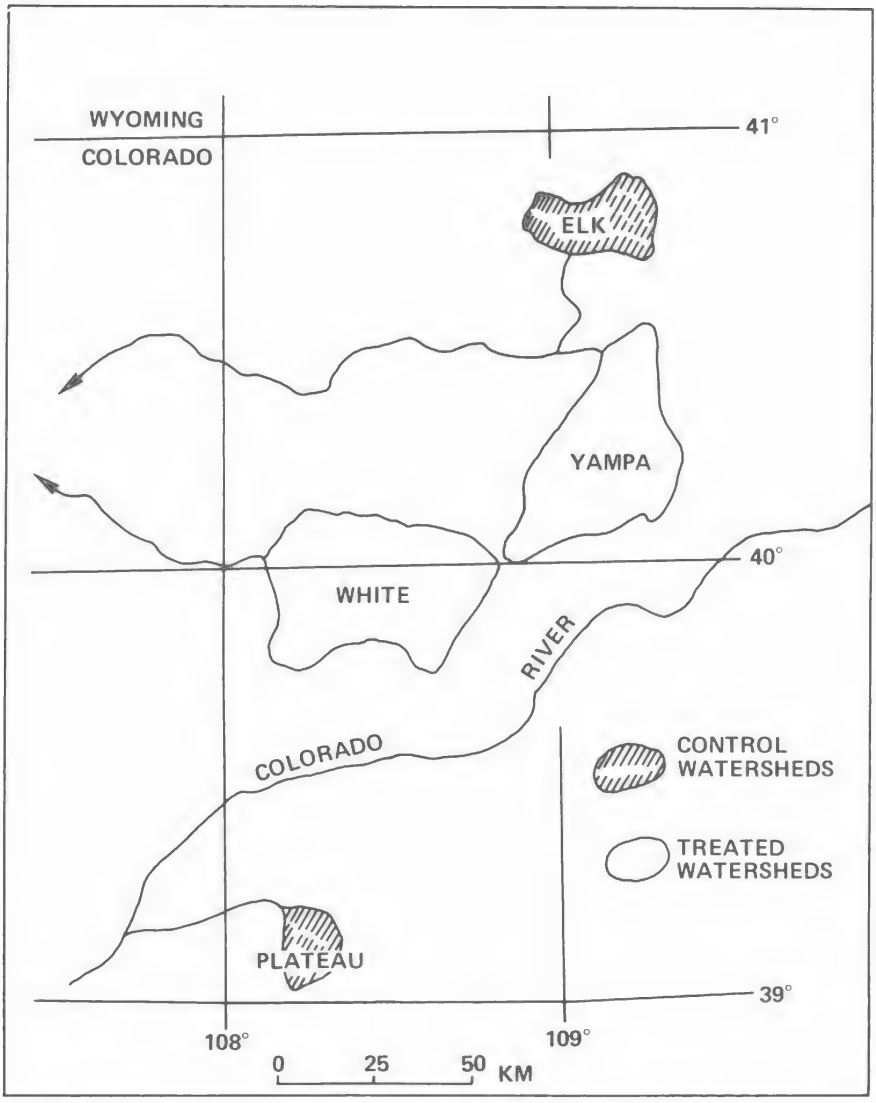


Figure 1. Location of studied watersheds. Only White and Yampa watersheds were affected by the beetle epidemic.

Elk and Plateau: the Unaffected Watersheds

Although the preceding analyses may be interpreted to mean that a change occurred in the water yields of the beetle-infested White and Yampa watersheds, one could also argue that identical results would be obtained if the control drainages (Elk and Plateau) yielded less water. These two drainages are approximately 190 km apart, and it is not reasonable to believe that a change would occur in the most widely separated water-

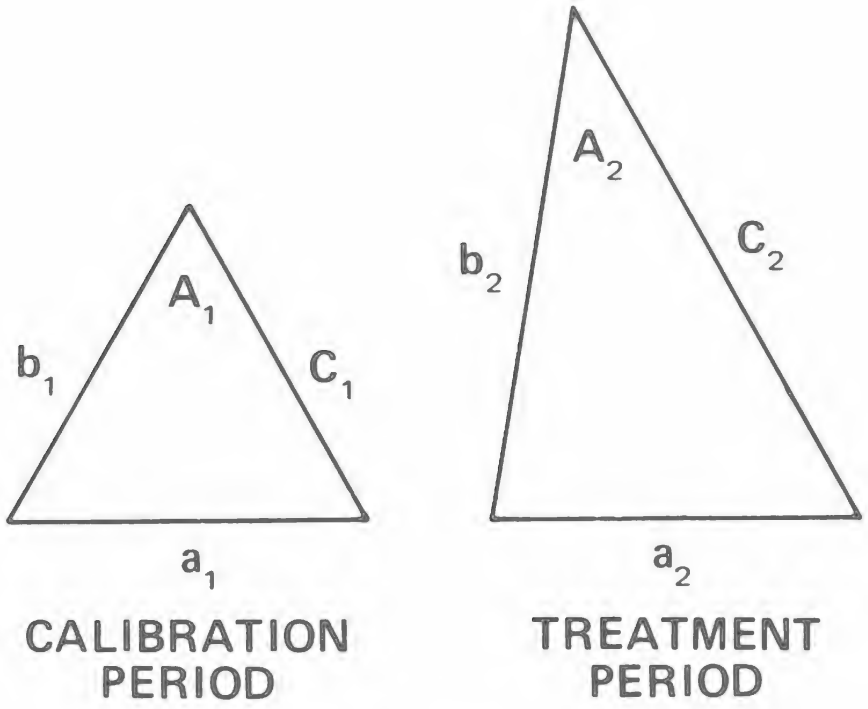


Figure 2. The integrating triangle method used to analyze and illustrate changes in relations among three watersheds. Base *a* represents the control watershed; sides *b* and *c* represent treated watersheds. Length of each side represents a river's measured variable expressed in terms of its average during the control period. Angle A_1 approximates 60° during control period, but will change significantly (A_2) if relations are altered among the watersheds.

sheds without also occurring in the two intervening watersheds. Accordingly, the hypothesis of increased water yields from the White and Yampa watersheds may be accepted if we show that the relation between Elk and Plateau remained constant during the pre- and postepidemic periods.

The relationship between water yields of Elk and Plateau is best studied by applying an analysis of covariance (Snedecor, 1948) to evaluate the significance of changes in either the regression coefficients or the adjusted means that characterize the regression lines of the pre- and postepidemic periods. The analysis revealed no change in the values of either the regression coefficients or the adjusted means ($F_{regression} = 0.70$; $F_{mean} = 0.91$). Therefore, one may safely conclude that runoff relationships between the two control watersheds remained constant during the period of study.

TABLE 1. Average vertex angle (radians) of runoff triangles[1] before and after the Colorado bark-beetle epidemic. Comparisons are for annual, high-month, October, and January runoff.

Period	Annual	High month[2]	October	January
	Triangle Base: Elk River Flows			
Pre-epidemic	1.047	1.047	1.039	1.045
Postepidemic	0.987	1.009	0.951	0.973
1946-50	1.004	1.028	0.976	1.036
1950-55	0.978	0.981	0.925	0.940
1956-60	0.966	1.000	0.938	0.962
1961-65	0.999	1.026	0.966	0.954
	Triangle Base: Plateau Creek Flows			
Pre-epidemic	1.045	1.049	1.035	1.045
Postepidemic	0.923	0.971	0.871	0.950
1946-50	0.986	0.990	0.891	1.006
1951-55	0.955	0.951	0.850	0.963
1956-60	0.922	0.974	0.853	0.946
1961-65	0.828	—	0.890	0.887

[1] Two sets of triangles: Elk-White-Yampa and Plateau-White-Yampa. Elk and Plateau watersheds escaped the epidemic, and their runoff constitutes a triangle's base. The length of each side represents the investigated runoff expressed in terms of its pre-epidemic average.
[2] High-month runoff is generally May or June.

Analysis of Annual Water Yields

The preceding analyses of two sets of data indicated that the relationship among three watersheds changed over time, and that the change was not caused by changes in the control watersheds—Elk and Plateau. The inference was that the change resulted from an increase in flow of either the White River or the Yampa River or of both. The question was readily resolved by individual analyses of covariance (Table 2). Results indicated that highly significant changes occurred in the yields of both the White and Yampa watersheds.

How much more water did the watersheds yield after the epidemic? The answer may be obtained by comparing annual flows measured during the postepidemic years to flows calculated on the basis of the pre-epidemic regression equations. Two estimates are available for each watershed because both the Elk and the Plateau watersheds served as controls in calculating the individual regression equations. Averages of the two independent estimates are shown in Table 3. Average annual increases appear to be substantial. Twenty-five years after the epidemic, annual water yields of the gaged watersheds are still approximately 10 percent greater than the expected yields.

Figure 3 illustrates the marked contrast between annual water yields of the control and epidemic-affected ("treated") watersheds. Three features are noteworthy: (1) the control watersheds exhibit reduced streamflow from 1947 to 1955, but the treated watersheds show gains during most of that period; (2) gains are curtailed sharply when yield of the control rivers is far below the long-term average; (3) the treated watersheds again show distinct gains when more moisture is available, as indicated by gains in the control rivers.

Seasonal Changes in Streamflow

(a) Flows during October

The hydrologic year starts in October, at which time streamflow is derived primarily from groundwater flows. Streamflow should increase if transpiration decreased during the preceding months. An analysis of October flows shows that streamflow did indeed

TABLE 2. Values of variance ratio F from analyses of covariance of annual, October, and high-month yields (in cm) for periods before and after the Colorado bark-beetle epidemic, and values of a and b in regression equation $Y = a + bX_i$.

Relation tested	Parameter tested: Regression coefficient	Parameter tested: Adjusted mean	Period characterized: Before		After	
	F	F	a	b	a	b
	Annual Yields					
Y (White) versus						
X_1 (Elk)	3.24	14.32**	6.81	0.34	3.91	0.46
X_2 (Plateau)	12.08**	13.12**	15.94	0.25	11.43	0.52
Y (Yampa) versus						
X_1 (Elk)	5.31*	9.36**	2.59	0.39	−3.31	0.56
X_2 (Plateau)	10.05**	6.52**	15.70	0.18	7.76	0.56
	October Yields					
Y (White) versus						
X_1 (Elk)	1.95	2.77	0.79	0.57	1.25	0.23
X_2 (Plateau)	0.00	4.71*	1.06	0.46	1.20	0.47
Y (Yampa) versus						
X_1 (Elk)	2.34	10.44**	0.14	0.37	0.10	0.55
X_2 (Plateau)	7.63*	5.74*	0.32	0.28	0.17	0.82
	High-Month Yields					
Ln Y (White) versus						
Ln X_1 (Elk)	0.46	6.97*	−1.10	0.99	−1.49	1.18
Ln X_2 (Plateau)	0.01	5.62*	0.07	0.65	0.21	0.67
Ln Y (Yampa) versus						
Ln X_1 (Elk)	0.59	2.62	−0.18	0.77	−0.81	1.02
Ln X_2 (Plateau)	0.48	2.29	0.86	0.45	0.54	0.63

*95 percent level of significance.
**99 percent level of significance.

TABLE 3. Average[1] change in annual, October, and high-month water yields of White and Yampa watersheds during the postepidemic period.

Period	Annual increase cm	Annual increase %[3]	October increase cm	October increase %	High-month[2] increase cm	High-month[2] increase %
	White River					
1946-50	3.46	13.5	0.04	3.1	1.44	20.7
1951-55	3.86	16.8	0.20	15.9	1.73	28.2
1956-60	5.17	21.0	0.20	14.8	1.29	18.0
1961-65	2.68	11.5	0.06	4.5	—	—
	Yampa River					
1946-50	2.89	12.4	0.22	39.1	0.26	2.9
1951-55	2.37	11.4	0.13	29.2	1.07	13.0
1956-60	6.30	27.8	0.14	29.4	2.26	24.8
1961-65	2.52	11.7	0.15	28.1	—	—

[1] Average of the two independent estimates based on Elk River and Plateau Creek regression equations.
[2] High-month flow is generally May or June.
[3] Percent of expected values based on pre-epidemic regression equations.

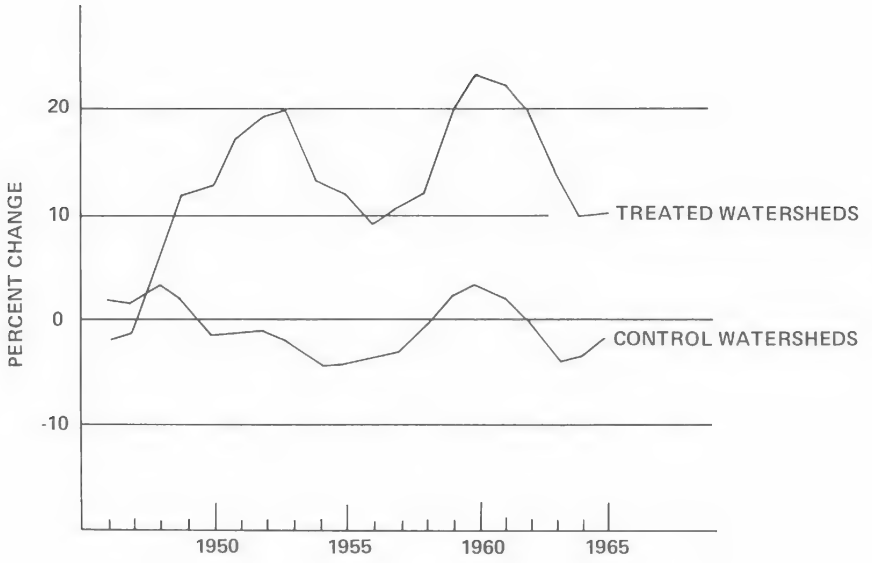


Figure 3. Five-year moving averages of change in expected yields of two groups of watersheds (each comprised of two watersheds) after a bark-beetle epidemic destroyed forests in the Treated Group but bypassed the Control Group.

increase after the epidemic. Integrating-triangle analyses (Table 1) showed that vertex angles decreased significantly (99 percent level of significance) and that more detailed analyses were warranted. Analyses of covariance (Table 2) revealed that after the epidemic, Yampa River yielded larger amounts of water (Table 3) but that White River flows changed significantly with respect to one control watershed (Plateau) but not with respect to the other (Elk).

Why did the two treated watersheds respond differently to the epidemic? The variable response was not caused by a change in the relationship of the two control watersheds; analysis of covariance showed that neither the regression coefficients nor the adjusted means that characterize their relationship changed during the period of study ($F_{regression} = 0.9$; $F_{mean} = 0.3$).

The variable response of the two treated watersheds may be understood if we consider the effect of exposure. This study is complicated by the fact that each of the considered rivers flows in a different primary direction (Fig. 1). The rivers that flow through the treated watersheds flow at almost right angles to each other and drain watersheds that differ greatly in their receipt of solar energy: Yampa River flows northward and drains a low-energy (LE) watershed that receives less heat than the high-energy (HE) White watershed that is drained by a westward-flowing river. Bethlahmy (1973) discussed the important characteristics that differentiate HE and LE watersheds; with these characteristics in mind, the variable response of the two treated watersheds is readily comprehended.

After the epidemic, October streamflow increases were greater on north-facing (LE) watersheds than on west-facing (HE) watersheds. During the 20-year period 1946-

1965, October flows on the LE watershed increased 0.16 cm (31.4 percent) in contrast to 0.12 cm (9.6 percent) on the HE watershed. We conjecture that the variable response of the two treated watersheds reflects smaller transpiration losses on the LE watershed and greater evaporation losses on the HE watershed.

(b) High-flow month

On the Colorado plateaus, winter precipitation occurs primarily as snow, and rivers flood in May and June when the accumulated winter snows melt. Annual runoff is closely related to spring runoff, as evidenced by the following highly significant correlation coefficients between annual runoff and flow during the month of highest runoff: Elk—0.94; Yampa—0.93; White—0.95; Plateau—0.90.

Logic dictates that if annual flows changed as a result of the beetle epidemic, then a concomitant change should have occurred in the high-month flows. Analysis of vertex angles (Table 1) showed that such was actually the case; the vertex angles diminished significantly (99 percent level of significance) when flows of Elk River and Plateau Creek were used successively as the triangle's base.

The importance of exposure again becomes evident in the individual analyses of covariance that showed an especially significant change in the west-flowing White River in contrast to the north-flowing Yampa. Average increases in yield during the 15-year period 1946-1960 were 1.49 cm (22 percent) for the HE White watershed and 1.20 cm (14 percent) for the LE Yampa watershed (Table 3).

(c) Flows during January

In the area studied, minimum flows generally occur in January. Analysis of vertex angles by the integrating-triangle method showed decreases significant at the 99 percent level of significance (Table 1). On the other hand, analyses of covariance showed that the change was limited to the White River.

White watershed is an HE watershed. In winter, only on such watersheds (in contrast to LE watersheds) would an opening in the forest canopy lend any advantage to radiation to increase snowmelt.

The ratio of January yields of White watershed to average yields of the control watersheds increased from 1.84 before the epidemic to 2.01 after the epidemic. Compare these figures to those at Wagon Wheel Gap, Colorado (Bates and Henry, 1928), where a 0.812 km^2 LE watershed (mean exposure N 68°E) was denuded of its forest cover and burned. Corresponding figures there (where minimum flows occur in February) were 1.207 and 1.216.

(d) Momentary peak flow

Rate and time of occurrence are two elements that characterize annual momentary peak flow—the maximum annual recorded instantaneous rate of flow.

White River's rates increased 27 percent (20.2 m^3/s), an increase significant at the 99 percent level of significance. In contrast, no such change occurred in the rate of north-flowing Yampa River; analysis of covariance showed that the apparent 4 percent increase was not significant.

The variable response of the two watersheds to the effects of the beetle epidemic is not surprising when exposure is considered as an additional element. During the

spring thaw, rate and time of occurrence of peak flows are controlled by regional and local weather conditions, and, in each watershed, exposure exerts a profound influence on incoming radiation.

Potential solar-beam irradiation (May 18, 50 percent slope) is approximately 825 langleys for Yampa watershed and 929 langleys for White watershed (cf. tables in Frank and Lee, 1966). Clearly, White watershed has an advantage of 12.6 percent with respect to incoming radiation that controls the rate of snowmelt. But two additional elements render this advantage particularly significant: more snow is available for melting because trees denuded of their branches and limbs intercept less snow, and additional storage space for snow is created when whole trees topple; and, if spring thaw is delayed (an occurrence that characterized the postepidemic period), the additional radiation on White watershed is particularly effective in melting the snow.

The following tabulation shows that during the postepidemic period all four watersheds peaked several days later than expected:

Watershed	*Day of momentary peak flow*	
	Before epidemic	*After epidemic*
Yampa	149	151
Plateau	142	147
White	145	156
Elk	143	153

The difference is particularly large for White and Elk, the two HE watersheds.

Results of the integrating-triangle method showed that values of the vertex angles did not change from one period to the other. On the other hand, results of individual analyses of covariance showed differences that are best interpreted in the light of contrasting exposures.

The following tabulation may explain the variable response of Yampa and White watersheds to the ravages of the beetle epidemic:

	Delay in peak flow days	*Level of significance* percent
HE versus HE watersheds		
White vs. Elk	+1	50
HE versus LE watersheds		
White vs. Plateau	+6	90
vs. Yampa	+9	95
Elk vs. Plateau	+5	75
vs. Yampa	+8	90
LE versus LE watersheds		
Yampa vs. Plateau	—3	50

Apparently peak-flow delays that approach an acceptable level of significance occur only between watersheds that have distinctly contrasting exposures.

Past research shows and logic suggests that opening a forest canopy will hasten, not delay, peak flow (Bates and Henry, 1928; Bethlahmy, 1973). But in this instance, general climatic conditions during the postepidemic period induced late peak flows in both HE and LE watersheds. Was the delay less prominent in the treated watersheds than in the control watersheds? The answer is "no" if we compare data from similarly exposed watersheds; neither the treated White nor the treated Yampa differ from their corresponding controls. We also infer that the general climatic conditions that induced universal late peak flows overshadowed the treatment effects and were more effective

on HE than on LE watersheds. We therefore conclude that exposure is a primary variable that should not be neglected in hydrologic analyses.

Discussion and Conclusions

This paper has dealt with the relationships between two groups of watersheds before and after a bark-beetle epidemic killed standing timber over vast areas in Colorado. The analyses indicate that a quarter of a century after the epidemic, the two affected watersheds still yield considerably more water than expected.

The explanation for the increased flows is not a change in climate. The four watersheds are in one climatic zone, and as indicated in one of the analyses, the relationship between the two most widely separated (and epidemic-spared) watersheds did not change during the two periods. A change in irrigation demands could explain the phenomenon, but public records do not support this conjecture.

The most logical explanation relates to vegetative cover. Before the epidemic, the forest consisted of mature and overmature trees that used water and functioned as a forest. After the epidemic, the dead trees no longer used water nor functioned in concert as a living forest with respect to the use of water.

Annual streamflow reflects the interaction of a watershed with its environment. The hydrology of the epidemic-affected watersheds changed because the component elements of the watersheds changed: "ghost" forests permit a greater accumulation of snow that in the spring melts to produce more water; water that dead trees do not pull from the earth seeps downward and appears as streamflow in summer and fall; the open canopy of the ghost forests permits the sun's heat to melt more snow in the winter.

The data presented are unique because of the large areas involved. They may also be unique in another way. We should not necessarily infer that similar results will follow all epidemics, whether insect or disease. Where forests consist of a large variety of species it is not likely that all trees will suddenly succumb to the same virulent agent. Also, natural regeneration may be prompt. Close to timber markets it is likely that the dead trees will be removed promptly; that young, vigorous seedlings will be established quickly; and that streamflow will revert to its pre-epidemic level in a modicum of time.

Literature Cited

Bates, C. B., and A. J. Henry. 1928. Forest and streamflow experiment at Wagon Wheel Gap, Colorado. USDA, Weather Bur., Mon. Weather Rev. Suppl. 30, 79 p., illus.

Bethlahmy, N. 1973. Water yield, annual peaks and exposure in mountainous terrain. J. Hydrol. 20: 155-169.

Bue, C. D., M. T. Wilson, and E. L. Peck. 1955. Discussion of "The effect on streamflow of the killing of spruce and pine by the Engelmann spruce beetle." Trans. Am. Geophys. Union 36(6): 1087-1089.

Frank, E. C., and R. Lee. 1966. Potential Solar Beam Irradiation on Slopes. U.S. For. Serv. Res. Pap. RM-18, 116 p., illus.

Hibbert, A. R. 1967. Forest treatment effects on water yield. P. 527-543, *in*: W. E. Sopper and H. W. Lull (ed.), Forest Hydrology. Pergamon Press. 813 p., illus.

Love, L. D. 1955. The effect on streamflow of the killing of spruce and pine by the Engelmann spruce beetle. Trans. Am. Geophys. Union 36(1): 113-118.

Patric, J. H. 1974. River flow increases in central New England after the hurricane of 1938. J. For. 72(1): 21-25.

Robinson, G. W. 1951. Soils. Their Origin, Constitution, and Classification. Thomas Murby & Co., London. 573 p., illus.

Snedecor, G. W. 1948. Statistical Methods. Iowa State Coll. Press. 485 p., illus.
Wygant, N. D., and A. D. Nelson. 1949. Four billion feet of beetle-killed spruce. P. 417-422, *in*: Trees, the Yearbook of Agriculture. U.S. Dep. Agric., Wash., D.C.

Received August 15, 1974.
Accepted for publication December 17, 1974.

Daniela L. Konicek

University of Puget Sound
Tacoma, Washington

Geophysical Survey in South Central Washington[1]

Abstract

Gravity survey, supplemented by available seismic, aeromagnetic and surface-geological data in the area shown on the Index Map (Fig. 1), reveals:
1. The problem eastern edge of the Cascade batholith.
2. A major mass excess along the Columbia River Gorge.
3. A gravity anomaly tentatively interpreted as a major fault striking N-S along the 120° W meridian.
4. Several sedimentary basins of potential significance for ground water exploration.

There is no gravity signature of the so-called Olympic-Wallowa Lineament, therefore, I conclude that this feature is neither a contact of two different crustal types nor a major fault as has been speculated.

Likewise, gravity signatures of the anticlinal ridges in that area are either faint or absent. The ridges thus seem to be confined to strata of constant density, probably basalt.

Introduction

The shaded area in Figure 1 shows the region covered by the present analysis. It includes the eastern slopes of the southern Cascade Mountains and the southwestern corner of the Columbia lava plateau. The boundary between the Cascades' mountainous terrain and the desert-type country follows approximately the 120°30′ meridian.

Several anticlinal ridges rising to an elevation of 2000 to 3000 ft cross the area in the approximate east-west direction (Fig. 2): Saddle Mountains, Manastash Ridge, Umtanum Ridge and Gable Mountains, Cowiche Mountain and Yakima Ridge, Ahtanum Ridge and Rattlesnake Hills, Toppenish Ridge with possible continuation in the Snipes Mountain, and the Horse Heaven Hills. Between those ridges are three prominent sedimentary basins: the Wenas, Yakima, and Toppenish basins (Waters, 1955). The Ellensburg Basin, at the northern edge of this survey, is bordered on the north by Wenatchee Mountains. The Pasco Basin is at the eastern edge of the survey.

Four of the above ridges are cut by the Yakima River, one by the Columbia River, and one by the Naches River. This relationship indicates that the river valleys antedate the rise of the anticlines. The rest of the drainage follows the synclinal troughs between adjacent ridges (Waters, 1955).

The structural geology of the area has been studied continuously since Russell's (1892) pioneering work:

a) *Manastash Ridge* is an asymmetrical anticline with steeper dips on the north limb (Smith, 1903).
b) The *Saddle Mountains* are a more complicated structure, in places tilted to the south, elsewhere overturned and thrust to the north (Laval, 1956; Smith, 1903).
c) *Umtanum Ridge* is an asymmetrical anticline with the northern dips steeper (Smith, 1903).

[1] This report is an abbreviated version of Koníček (1974); the full text, including the principal facts of the gravity survey, are in the files of the University of Puget Sound, Tacoma, Washington 98416.

Figure 1. Index map.

d) *Gable Mountain* is probably a remnant of a minor fold between the Saddle Mountains and the Rattlesnake Hills (Russell, 1892).
e) *Cowiche Mountain* and *Yakima Ridge* are two names for the same geologic feature, separated by the Yakima River Valley. Yakima Ridge is less continuous than the rest. (Waters, 1955).
f) *Ahtanum Ridge* and its eastern extension, *Rattlesnake Hills*, are a faulted anticline with the fault breccia exposed at the east and west ends of the northern slope. Like the Umtanum Ridge, Ahtanum Ridge probably extends farther west (Laval, 1956; Smith, 1903).
g) *Toppenish Ridge* is a composite anticline with subsidiary anticlinal flexures. On its northern flank are two large recent landslides that may have tectonic implications (Laval, 1956).
h) *Snipes Mountain* is an asymmetrical anticline with a steeper southern limb (Laval, 1956).
i) *Horse Heaven Plateau* and its northern flank, the *Horse Heaven Hills*, are the largest anticlinal structure of the entire Columbia Basin (Laval, 1956).

The idealized geological column is taken from Russell (1892), Smith (1903), Huntting (1961), Mackin (1961), Bingham and Grolier (1966), Brown (1969) and Wright *et al.* (1973), and is shown in Figure 3. The thicknesses, of course, vary from place to place so that the values reported in Figure 3 give only their order of magnitude. Most authors describe in detail only the post-Eocene formations. Because the densities of basalts of various ages are nearly identical, the basalt slab is considered as a single lithologic unit for gravity interpretations.

The total thickness of the basalts is unknown. Brown (1969) reports at least 10,000 ft (3100 m) in the Rattlesnake #1 well, but this value is certainly conservative since the bottom of the basalt slab had not been reached.

In the northern part of the Columbia Plateau, the basalts rest on acidic crystalline rocks, providing a density contrast of at most 0.3 gm/cm^3. A similar contrast in the

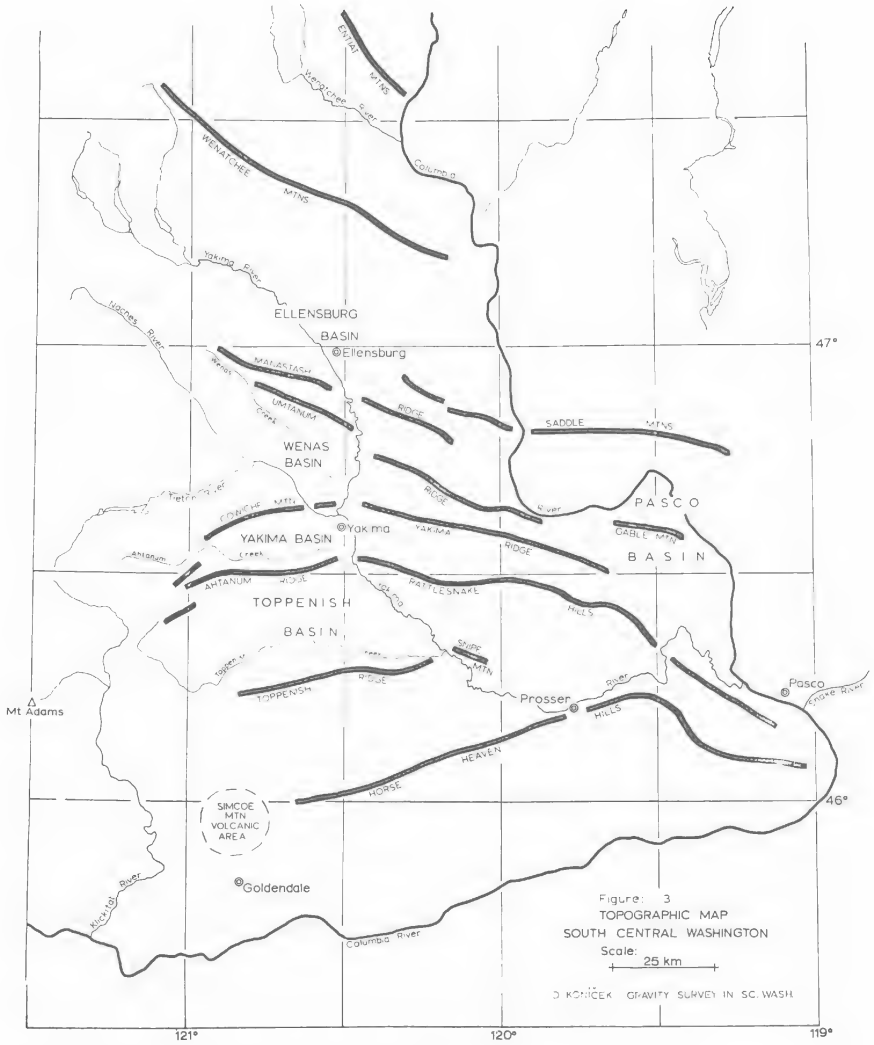


Figure 2. Topographic map of south central Washington.

area under consideration seems to be probable from data presented in the Interpretation.

Raisz (1945) noticed an interesting linear topographic feature stretching from the Olympic Mountains deep into Idaho and gave it the name of "Olympic-Wallowa-Lineament." In the following discussion this name is abbreviated as O-W-L. While Raisz himself was only speculating about the significance of that feature, Skehan (1967), using the deep resistivity data of Cantwell, Nelson, and Webb (1965), and Cantwell and Orange (1965), as well as Skehan's own geological survey, interpreted the

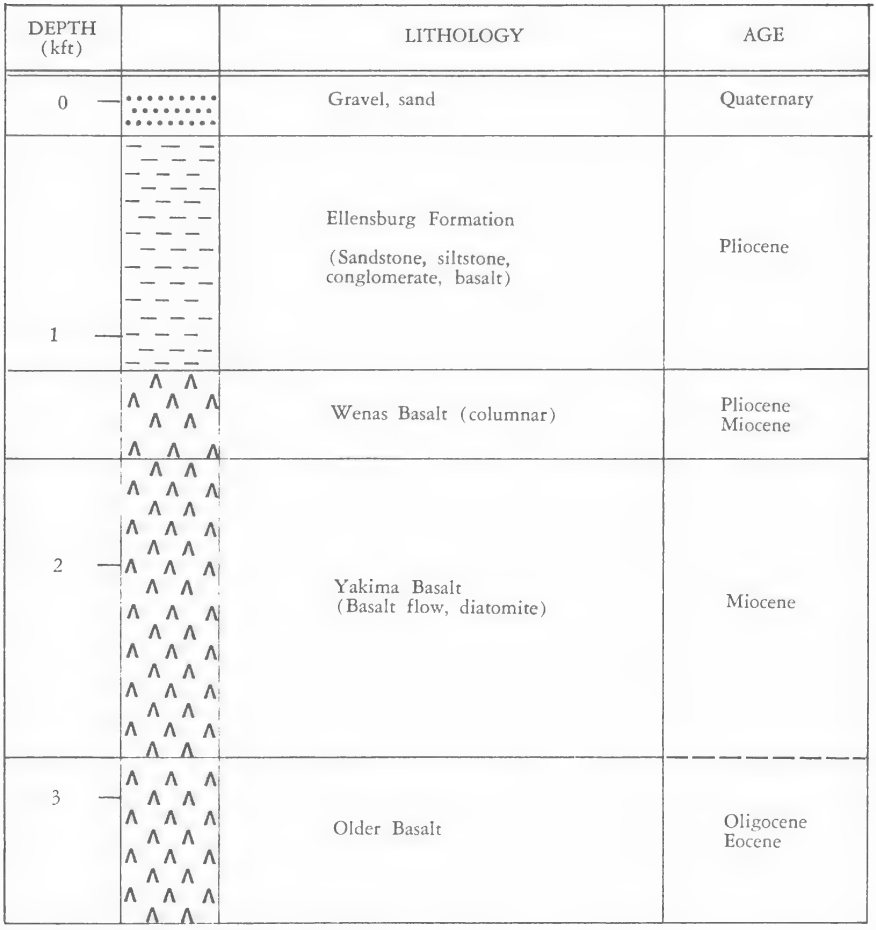


Figure 3. Idealized geological column.

lineament as a contact between the oceanic and continental crust. As stated in the Interpretation, my results are at variance with Skehan's.

The western part of my survey extends into the young volcanic centers of Mt. Adams, Mt. St. Helens, and the Simcoe Mountains (Sheppard, 1967). This region is currently being investigated by Hammond (1973), Pedersen (1973), and Stricklin (in progress). Their results indicate that a large amount of olivine basalt was erupted from a northwest-trending line of shield volcanoes between the westward extension of Horse Heaven Hills and the Toppenish Ridge and this basalt became localized in the synclinal valley between the two ridges.

A detailed gravity survey of the Toppenish and Yakima Basins has been conducted by the U.S. Geological Survey (Robbins *et al.,* 1973) to assist in ground water exploration. Those data were not available for inclusion in my survey, therefore my field work duplicated the U.S. Geological Survey work on a more open grid.

Although numerous seismic epicenters have been reported north, west, and south of the area of this report, no present earthquake activity is known in the region.

Magnetically, the area was surveyed by Zietz *et al.* (1971). The results are discussed in the Interpretation.

Field Work and Reductions

The gravity survey was conducted between June 6, 1972 and September 9, 1972 by means of geodetic Worden gravity meter #358. Over an area of about 15,000 km^2 516 stations were established, thus resulting in average station spacing of 5-6 km. The survey was tied into the Army Map Service Gravity Base Station Network (1967).

At least one base reading was taken each day of field work, and the beginning and the end of each loop were tied in. When possible, several base readings were taken per day. Most stations were located at available bench marks. In most cases, the error in the elevations of stations occupied does not exceed $\pm$ 1 ft.

Standard station reduction density of $\rho =$ 2.67 gm/cm^3 was used for the elevation correction. This density is probably too low for the basaltic ridges and too high for the alluvium. Therefore, another Bouguer gravity map with station reduction density of $\rho =$ 2.92 gm/cm^3 (not included) was also derived. The difference in interpretation was negligible, and I feel that the 2.67 gm/cm^3 density is adequate.

Terrain corrections were derived by Hammer's (1939) method and carried out to his zone J. In many cases, the terrain of long parallel ridges is, for all practical purposes, "two dimensional"; for those cases, a simplified chart was prepared and used. The more distant mountains produce an additional terrain effect of the order of a few milligals, but that correction is rather smooth and would only superpose a gently sloping regional correction which would not modify my interpretation.

The overall reliability of the gravity data is of the order of a fraction of a milligal in the lowlands, and a few milligals in the mountains.

The survey was tied into Peterson's (1966 and 1968) data to the west, Berg's and Thiruvathukal's (1967) results to the south, and Bonini *et al.* (1974) elsewhere.

Results

Results of the analysis are presented on the Bouguer Gravity Map (Fig. 4), the Residual Gravity Map (Fig. 5), and the profiles A - A′ and B - B′ (Figs. 7 and 8).

Residual Gravity was derived from the Bouguer Gravity by subtracting a smooth regional anomaly.

Gravity results are supplemented by Aeromagnetic Map (Fig. 6 reproduced from Zietz *et al.* (1971)). The magnetic anomalies are also shown on the two profiles (Figs. 7 and 8). Magnetic data were taken at a flight elevation of about 15,000 ft (5 km) above ground.

The Bouguer Gravity values range from a maximum of -38.3 mgal 10 km northeast of Prosser to -119.0 mgal about 25 km northeast of Mt. Adams. The transition takes place in two major steps of change in values of about 40 mgal each, striking north-south; one in the vicinity of 120° W, the other near 121° W. At about 46° N, the strike of the gravity contours changes from north-south to approximately east-west.

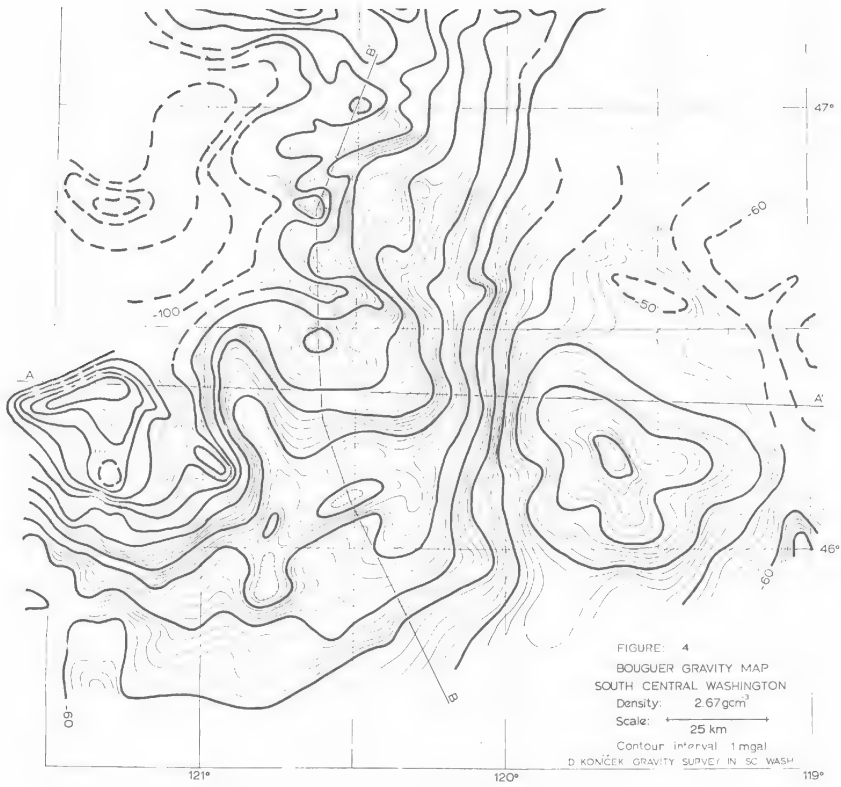


Figure 4. Bouguer gravity map of south central Washington.

Interpretation

The gravity anomalies in the area can be divided into two groups: the major regional features, and the local ones.

The major features include:

1. The steep gradient striking approximately north-south along 121° W meridian (Fig. 4). This is probably representative of the eastern edge of a batholith underneath the Cascade Mountains. The steepness of the gradient indicates that the batholith is fairly close to the surface, covered only by a thin layer of recent volcanic rock. If this is so, and if the anomaly is due to the juxtaposition of acidic rocks and basalt, then the density contrast is about 0.25 gm/cm^3, and the area east of 121° W must be covered by a basalt slab several kilometers thick (Fig. 7). According to Swanson and Robbins (personal communication), the density contrast may be actually less than 0.25 gm/cm^3 so that the basalt thickness would have to be even greater.

2. The gradient striking north-south along the 120° W (Fig. 4) is more gentle. Theoretically, it may be due to a shallow density contrast along an easterly-dipping plane. However, since basalts are known to be west of the 120° W meridian, and since I know of no rock-type in that area that would be heavier than basalt, I consider

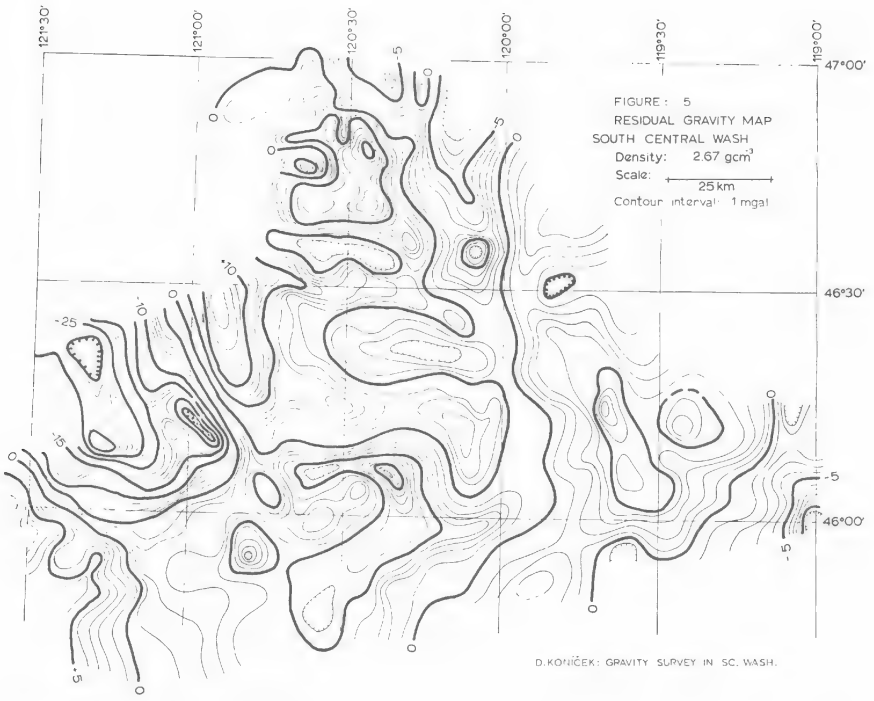


Figure 5. Residual gravity map.

this interpretation as untenable. The other possibility is a contact at a greater depth. The most likely density contrast in this area is the 0.25 gm/cm^3 between the basalt and the underlying basement. This value was used in a computer program designed to evaluate the subsurface mass distribution. Results of the analysis are shown in Figure 7, where the heavy, solid line represents the Bouguer anomaly as taken from the map (Figure 4), crosses are station values in the vicinity of the profile, and circles are values from the computer program. In spite of the good agreement between calculated and observed values, the interpretation, of course, is not unique. Nevertheless, the total basalt thickness is probably correct, especially since it is in good agreement with the estimate of Cantwell *et al.* (1965).

A question can be raised whether the basalts have any bottom at all or whether they communicate with the upper mantle. I believe that they do not communicate, because if they did the Bouguer gravity anomaly would be of the order of +50 mgal, similar to that in the Coast Range. It seems more probable that the basalts rest on a layer of continental crust extending to a depth of the order of 20 km.

Toward the east of about 119°30′ W, the thickness of the basalts seems to decrease, but present gravity data are not adequate to permit quantitative interpretation (Fig. 7). Additional remarks on this feature follow the interpretation of local anomalies.

3. The east-west gradient along the 46° N follows the Columbia River Valley and Gorge (Fig. 4). I suspect that this anomaly is representative of a major tectonic

break between the Washington and Oregon Cascades and that the Columbia drainage in that area is secondary. It is probably significant that it was here that Cantwell

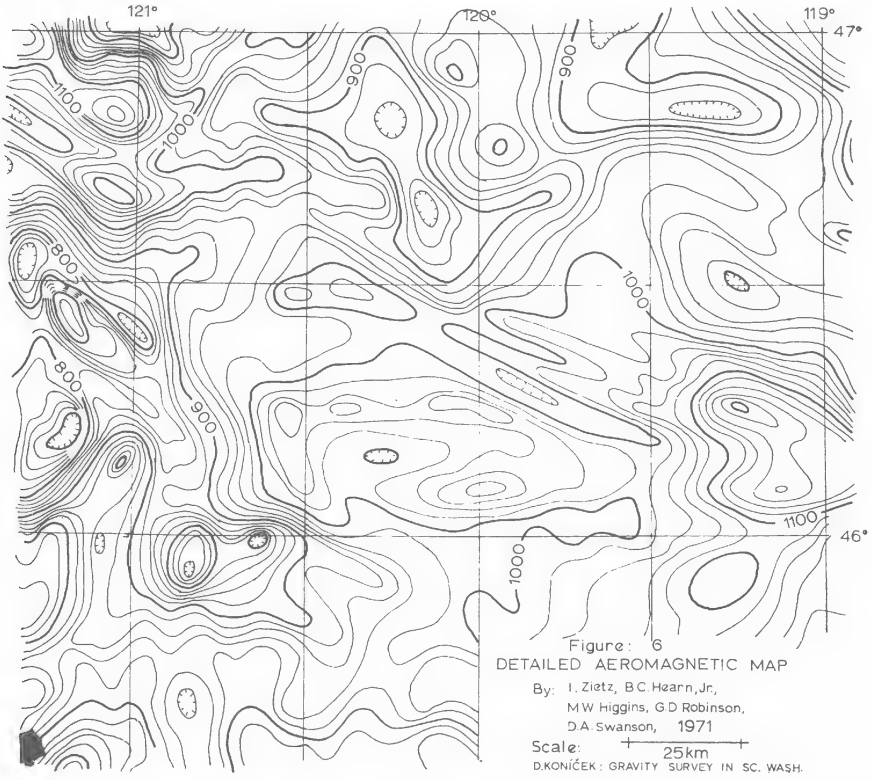


Figure 6. Detailed aeromagnetic map.

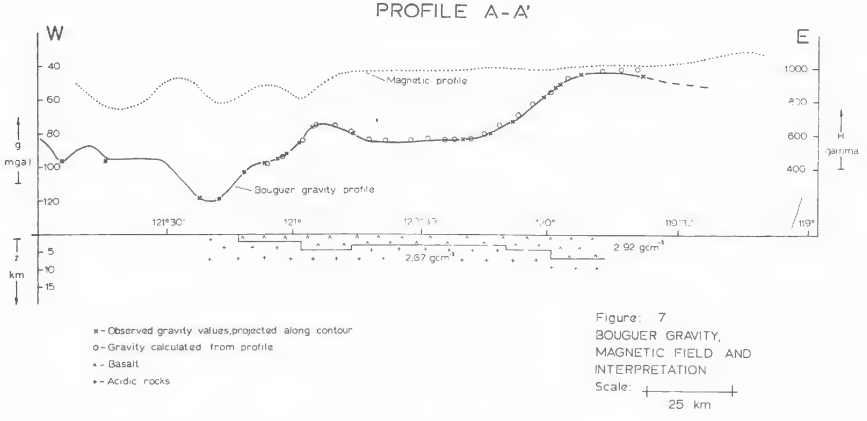


Figure 7. Bouguer gravity, magnetic field, and interpretation.

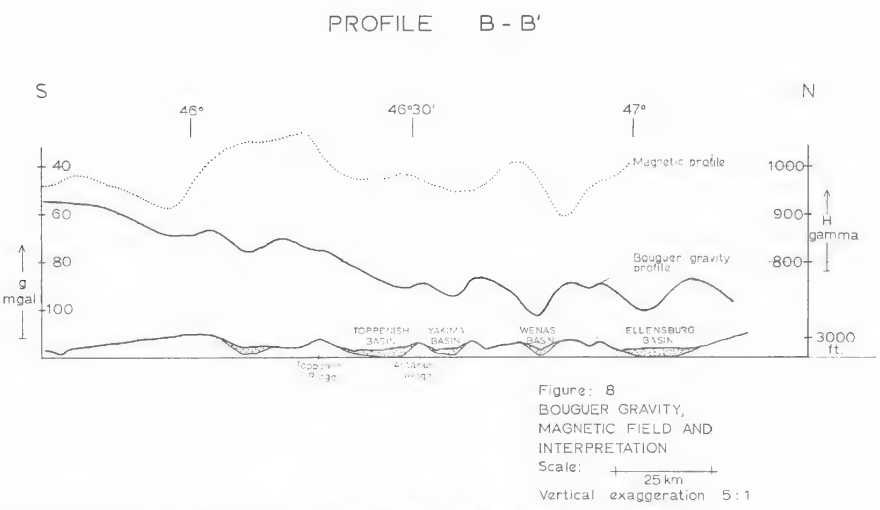


Figure 8. Bouguer gravity, magnetic field, and interpretation.

et al. (1965) found a major resistivity change. Unfortunately, their results are based on stations too far apart to identify the changes more precisely.

4. The only gravity anomaly that shows any resemblance to the O-W-L is the gradient along the eastern portion of Rattlesnake Hills (Fig. 4). This, however, seems to be just a local feature and has no continuation farther northwest. I thus conclude that the O-W-L is neither a contact of oceanic vs. continental crust, nor a major fault (Skehan, 1965).

On the local scale, the gravity and magnetic signatures of topographic features are listed in Table 1.

There is a good overall correlation between local gravity minima and known recent sedimentary basins. I assumed a density contrast between the sediments and the underlying basalt to be about 0.7 gm/cm^3 (Fig. 8). It may be significant that all the bottoms of those basins are at approximately the same depth and very close to present sea level. An exception to this rule is the Pasco Basin, where a gentle gravity high is indicated. This area requires additional field work. According to Robbins (personal communication), the 0.7 gm/cm^3 density contrast may be too high and 0.5 gm/cm^3 may be more realistic.

Since the study area is arid, and since those basins are drained by streams fed by the snow of the Cascade Mountains, my result may be of considerable interest in connection with the problem of ground water exploration (Robbins *et al.*, 1973).

On the other hand, correlation between topographic and structural ridges on the one hand and gravity and magnetics on the other is, generally, poor. The only ridge associated with a clear gravity high is Gable Mountain; since this ridge rises from the Pasco Basin, I believe that it is partly buried by sediments, and that the gravity high is due to the density contrast between the basalts and the sediments, rather than to a contrast within the structure.

Gravity anomalies of other ridges, if any, are harder to interpret. Manastash

TABLE 1. Table of the relation between the gravity and magnetic data.

FEATURES	GRAVITY DATA	MAGNETIC DATA
Manastash Ridge	none	weak
Umtanum Ridge	positive in western part	positive, + 70 gamma
Saddle Mountains	not defined	negative, – 50 gamma, displ. to the north in eastern part
Cowiche Mountains	positive, offset 5 km to the north	negative, – 50 gamma displ. to the south 7 km
Yakima Ridge	none	eastern part no signature; some sign. in western part
Gable Mountain	positive, + 5 mgal	none
Ahtanum Ridge	positive, +5 mgal	? ? ?
Rattlesnake Hills	positive west of 120°, + 4 mgal; no express. east of there	positive, + 30 gamma, displ. 10 km to the south
Toppenish Ridge	positive, + 5 mgal, displ. toward south	positive, + 30 gamma, displ. 7-8 km to south
Snipes Mountain	? ? ?	same as Toppenish Ridge
Horse Heaven Hills	? ? ?	positive in extreme east
Ellensburg Basin	negative, – 10 mgal	positive, + 50 gamma
Wenas Basin	negative, – 10 mgal	positive, + 50 gamma
Yakima Basin	negative, – 5 mgal	positive, + 30 gamma
Toppenish Basin	negative, – 10 mgal	negative, – 20 gamma
Pasco Basin	positive, + 10 mgal	positive, + 50 gamma

Ridge has virtually no gravity signature and only a week magnetic high in the western portion. Umtanum Ridge, Cowiche Mountain, Ahtanum Ridge, Rattlesnake Hills, and Toppenish Ridge are associated with the gravity maxima in some parts, but those maxima are offset by several kilometers north or south. This may be due to a tilt at right angles to their strike so that most of the mass excess of each ridge may be a fair distance from the visible crest; but it may also be due to mass anomalies unrelated to the tectonic features.

In this connection, however, it may be significant that the correlation between gravity and structure changes quite abruptly in the vicinity of 120° W gradient. In particular, the gravity maximum associated with Rattlesnake Hills (Fig. 5) terminates at that longitude but exhibits a sudden bend toward the south. A similar bend is also indicated by the strike south of the Snipes Mountain but the gravity signature is much more pronounced.

Furthermore, it may be significant that the Wenatchee Mountains, Manastash Ridge, and Snipes Mountain show no continuation east of the 120° W gradient, and that the Columbia River drainage in that area follows the 120° W meridian quite closely for a distance of 160 km. With a little imagination, this trend may be extrapolated into the Okanogan Valley for another 100 km or more, and correlates well with a series of recent seismic epicenters along the eastern foothills of the Cascade Mountains (Rasmussen, 1969). I, therefore, speculate that there may be a major right-lateral fault along the 120° W meridian, and that the anticlinal ridges mentioned above may be a result of the compressional component of the same stress tensor that produced the fault. If it is so, then there should be some evidence of a tensile component in the northwest-southeast direction; Farkas and Bentley (oral communication) inform me that such evidence may have been found in the Yakima River Valley between Ellensburg and Yakima.

A stress of that kind would be compatible with the northward drift of the Pacific Plate with respect to the North American Plate.

A pronounced gravity low of about -8 mgal correlates well with the Simcoe Mountains' volcanic area (Sheppard, 1967) and with a -200 gamma magnetic low (Zietz *et al.*, 1965). This feature, too, deserves further investigation.

An interesting gravity high, striking N15°W is centered at 120°55'W, 46° 25'N. It may be due to a buried ultramafic body similar to other such features along both the eastern and western foothills of the Cascades. This interpretation may be corroborated by the -150 gamma magnetic low (Fig. 6). On the other hand, this feature may also be interpreted as due to a local thickening of the basalts. The quantitative results based on the latter assumption are shown in Figure 7.

Conclusions

Results of this analysis may be summarized as follows:

1. The O-W-L is neither a contact of oceanic and continental crust, nor a major fault.

2. The thickness of the basalts increases in several steps to a total thickness of about 8 km in the vicinity of Prosser.

3. Five basins have a sedimentary layer of about 0.5 km in thickness, which may be significant for ground water exploration.

4. Gravity signatures of anticlinal ridges are weak; the anticlines, therefore, seem to be confined to strata of constant density (basalt?).

Acknowledgements

My thanks are expressed to the Research Corporation (Dr. Hal H. Ramsey) for financial support; to Mr. Donnel Hoffman for his help in the field; to the Yakima Indian Nation for permission to carry out the survey within their territory; to Dr. Bert Brown and L. Corp. Peter Daneš (USMC) for writing computer programs; to Drs. Robert Bentley, Steve Farkas, Dan Brown, D. D. Tillson, Paul E. Hammond, and Mr. Steve Pedersen for advice in interpretation; to Drs. Norman Anderson and Albert A. Eggers for reviewing the manuscript; to Miss Helen Ahrens for typing and linguistic corrections; and to my thesis advisor, Dr. Z. F. Daneš, for his help and direction.

Literature Cited

Anonymous. 1942. Theoretical Gravity of Sea Level for Each Minute of Latitude by the International Formula. U.S. Dept. of Commerce, Coast and Geodetic Survey, Washington, D.C.

Army Map Service. 1967. Washington Gravity Base Station Network. U.S. Army Corps of Engineers, Army Map Service, Washington, D.C.

Berg, J. W., and J. V. Thiruvathukal. 1967. Complete Bouguer Gravity Map of Oregon. State of Oregon, Dept. of Geology and Mineral Industries, Portland, Oregon.

Bingham, J. W., and M. J. Grolier. 1966. The Yakima Basalt and Ellensburg Formation of South Central Washington. U.S. Geol. Survey Bull., 1224-G, p. 61-65.

Bonini, W. E., D. W. Hughes, and Z. F. Daneš. 1974. Complete Bouguer Gravity Anomaly Map of Washington. Dept. of Natural Resources, Olympia, Washington.

Brown, R. E. 1969. Some suggested rates of deformation of the basalt in the Pasco Basin, and their implications. Proceedings of the Second Columbia River Basalt Symposium. p. 179-187.

Cantwell, T., P. Nelson, and J. Wegg. 1965. Deep resistivity measurements in the Pacific Northwest. Jour. of Geophysical Res. 70 (8): 1931-1937.
————, and A. Orange. 1965. Further deep resistivity measurements in the Pacific Northwest. Jour. of Geophysical Res. 70 (16): 4048-4072.
Hammer, S. 1939. Terrain Corrections for Gravimeter Stations. Geophysics 4: 184-194.
Hammond, P. E. 1973. Quaternary Basaltic Volcanism in the Southern Cascade Range, Washington. Cordilleran Section 69th Annual Meeting, The Paleontological Society, Pacific Coast Section.
Koníček, D. L. 1974. Geophysical Survey in South Central Washington. Univ. of Puget Sound. Master's thesis.
Laval, W. N. 1956. Stratigraphy and Structural Geology of a Portion of South Central Washington. Univ. of Washington, Ph.D. thesis, Geol.
Mackin, J. H. 1961. A stratigraphic section in the Yakima Basalt and the Ellensburg Formation in South Central Washington. Wash. Div. of Mines and Geology. Report of Investigations, No. 19. Olympia, Wash.
Pedersen, S. A. 1973. Intraglacial Volcanoes of the Creasy Hills Area, Northern Skamania County, Washington. Cordilleran Section 69th Annual Meeting, the Paleontological Society, Pacific Coast Section.
Peterson, D. E. 1966. Variations in the Earth's gravity field at Hanford. Pacific Northwest Laboratory Annual Report for 1965 in the Physical Sciences to the USAEC Div. of Biology and Medicine, vol. 3, Earth Science, p. 4-13.
————. 1968. Bouguer Gravity Anomalies on the Hanford Reservation. Pacific Northwest Laboratory Annual Report for 1966 to the USAEC, Div. of Biology and Medicine, vol. II, Physical Sciences, Part 3, Earth Sciences, p. 10-11.
Raisz, E. 1945. The Olympic-Wallowa-Lineament. Amer. Jour. of Sci. 243-A: 479-485.
Rasmussen, N. H. 1969. Seismic Trends in Washington State. Univ. of Wash, Earthquake Engineering Group, Seattle, Wash.
Robbins, S. L., R. J. Burt, and D. O. Gregg. 1973. Gravity and Aeromagnetic Study of Part of the Yakima River Basin, Wash. U.S. Geol. Survey, Professional Paper (to be published).
Russell, E. C. 1892. Geology reconnaissance in Central Washington. U.S. Geol. Survey Bull., No. 108, p. 13-108.
Sheppard, R. A. 1967. Geology of the Simcoe Mountains volcanic area, Washington. Wash. State Div. of Mines and Geology, Geology Map GM-3.
Skehan, V. W. 1965. A continental oceanic crustal boundary in the Pacific Northwest. U.S. Air Force, Cambridge Res. Lab., No. 65-904, p. 56.
Smith, G. O. 1903. Anticlinal Mountain Ridges in Central Washington. Jour. of Geology XI (2): 166-177.
Stricklin, Claude R. Geophysical (Gravity) Survey of the Sawtooth Mountain Area in the South Cascade Mountains of Washington. Univ. of Puget Sound, Master's thesis (in progress).
Waters, A. C. 1955. Geomorphology of South Central Washington, Illustrated by the Yakima East Quadrangle. Bull. of Geol. Soc. of America 66: 663-684.
Wright, T. L., M. J. Grolier, D. A. Swanson. 1973. Chemical Variation Related to the Stratigraphy of the Columbia River Basalt. Geol. Soc. Amer. Bull. 84 (3): 371-385.
Zietz, I., B. C. Hearn, Jr., M. W. Higgins, G. D. Robinson, D. H. Swanson. 1971. Interpretation of an Aeromagnetic Strip Across the Northwestern United States. Geol. Soc. Amer. Bull. 82 (12): 3347-3371.

Received June 28, 1974.
Accepted for publication December 9, 1974.

Grant A. Harris
Dept. For. & Range Mgt.
Washington State Univ.
Pullman, WA 99163

Northwest Science

Earl E. Nelson
and
Harlan A. Fay

Pacific Northwest Forest and Range
Experiment Station
Forest Service, U.S. Department of Agriculture
Corvallis, Oregon

Effect of Temperature on Growth and Survival of High- and Low-Elevation Isolates of Phellinus (Poria) weirii

Abstract

Isolates of *Phellinus weirii* (Murr.) Gilbertson (*Poria weirii*) from above 1,675-m elevation did not differ significantly from those below 488 m in growth or survival under various temperature regimes. The fungus generally survived from −5° to 32° C for up to one year. Linear growth was generally best at 25° C, followed by 20°, 15°, 30°, 10°, and 5° C.

Introduction

Phellinus weirii (Murr.) Gilbertson (*Poria weirii*) causes a severe root disease of western conifers in diverse habitats. Recent measurements of rate of disease development at elevations exceeding 1,524 m in Oregon's Cascade Range showed a radial extension of infection centers averaging 34 cm per year (Nelson and Hartman, 1975). This is somewhat greater than that estimated for Douglas-fir at lower elevations (Childs, 1970).

To determine if differences existed between high- and low-elevation isolates of *P. weirii* in their ability to grow and survive in the laboratory over a range of temperatures, we tested five isolates of the fungus from above 1,675 m and five isolates from elevations between 137 and 488 m.

Methods and Materials

Isolates of *P. weirii* were obtained from Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) in the Cascade Range and Olympic Peninsula of western Washington (T-isolates) and from Mountain hemlock (*Tsuga mertensiana* [Bong.] Carr) in the Cascade Range of western Oregon (W-isolates).

Isolate number	*Elevation*	*Location*
T-55	488 m	near Randle, Wash.
T-65	335 m	near Carson, Wash.
T-102	137 m	near Elma, Wash.
T-122	380 m	near Quilcene, Wash.
T-125	380 m	near Quilcene, Wash.
W-1, W-4, W-9, W-12, W-13	1,675-1,677 m	Willamette National Forest near Waldo Lake, Oregon

All W-isolates had been held in culture on malt agar at 2° C for nearly two years. T-isolates had been held similarly for more than ten years. All isolates were grown on malt agar in petri plates.

Linear Growth Study

From the leading edge of colonies of each isolate growing on malt agar, 4-mm-diameter disks were taken with a cork borer and transferred to centers of petri plates containing 30 ml of the same growth medium. Three replicate plates were incubated at 5°, 10°, 15°, 20°, 25°, and 30° C and colony diameters measured to the nearest millimeter at daily or less frequent intervals, depending upon rate of growth at a particular temperature. Growth of each isolate over time was plotted for each temperature, and rates of growth (over the linear portion of the curve) were compared.

Survival Study

Each isolate was grown on autoclaved red alder disks (6 to 8 mm in diameter and about 3 mm thick) loosely arranged over gravel and water in 60 ml-capacity French Square bottles. Forty disks were placed in each bottle, and three bottles for each isolate were incubated at –20°, –15°, –10°, –5°, 2°, 25°, 30°, 32°, and 34° C. After 0, 1, 2, 4, and 8 days and 2, 4, 8, 16, 24, 32, 42, and 52 weeks of incubation, three disks were removed from one of the bottles for each isolate at each temperature and plated on malt agar at room temperature to determine viability of the fungus. The two remaining bottles for each isolate at each temperature were used only if the first became contaminated or dried out, or to substantiate loss of viability when it occurred in the first bottle.

Results and Discussion

Linear Growth Study

Growth of all isolates was best at 25°, followed by 20° and 15° C. For the remaining three temperatures, growth was best in seven of 10 isolates at 30° followed by 10° and 5° C; three isolates grew best at 10° followed by 5° and 30° C (T- 55, W-4, and W-12). Li *et al.* (1967), using a single isolate of *P. weirii,* found no growth at 30° C and optimum growth at 20° C as compared with optima of 25° C in this study. Average growth rate of low-elevation isolates was better than that of high-elevation isolates except at 5° C (Table 1), but there were no statistically significant differences in growth between the two groups ($p = .05$) when compared by analysis of variance at each temperature or by regression.

TABLE 1. Average daily increase in colony diameter of high- and low-elevation isolates of *Phellinus weirii* on malt agar.

Elevation group	Incubation temperature (Centigrade)					
	5°	10°	15°	20°	25°	30°
	mm					
Low (T)	3.42	4.86	12.52	15.34	19.04	5.60
High (W)	3.82	4.76	11.98	14.58	18.52	4.90

Survival Study

Phellinus weirii survived in all cases for a year at temperatures from –5° to 30° C and to 32° C in all but one clone (T-55). Survival among clones of the fungus varied little at other temperatures and times observed. Most of that variation occurred at –20°, –15°, and –10° C, and survival at these temperatures did not exceed four weeks in any case. Only one clone (W-13) failed to survive at least four days at –20° C. There appeared to be no difference in survival between high- and low-elevation clones at the times and temperatures observed. Survival was somewhat poorer than that reported earlier for another clone of *P. weirii* in larger alder stem sections (Nelson and Fay, 1974).

The two groups of isolates of *P. weirii* tested here were from diverse habitats (different latitudes, elevation ranges, soil origins, and hosts) and had been held in storage for different lengths of time. Even so, they appeared to have as much variation in growth and survival within groups as between them in response to the experimental conditions of time and temperature. Greater variation between groups might be difficult to explain since the fungus in general appears to grow and survive over a wide range of temperatures as well as in a diversity of soils, host species, and geographic and climatic extremes.

Literature Cited

Childs, T. W. 1970. Laminated root rot in western Oregon and Washington. USDA For. Serv. Res. Pap. PNW-102, 27 p., illus. Pac. Northwest For. & Range Exp. Stn., Portland, Oreg.

Li, C. Y., K. C. Lu, J. M. Trappe, and W. B. Bollen. 1967. Effect of pH and temperature on growth of *Poria weirii* in vitro. USDA For. Serv. Res. Note PNW-66, 6 p. Pac. Northwest For. & Range Exp. Stn., Portland, Oreg.

Nelson, E. E., and H. Fay. 1974. Thermal tolerance of *Poria weirii*. Can. J. For. Res. 4: 288-290.

————, and T. Hartman. Estimating spread of *Poria weirii* in a high elevation, mixed conifer stand. J. For. 73(3):141-142.

Received March 18, 1975.
Accepted for publication May 7, 1975.

R. Daubenmire

Department of Botany
Washington State University
Pullman, Washington

An Analysis of Structural and Functional Characters along a Steppe-Forest Catena

Abstract

Quantitative analyses of the stable types of vegetation of zonal soils along an altitudinal transect, starting in very dry steppe and ending in cold, wet, subalpine forest, provided species lists used in this study. This vegetation catena has been analyzed according to species diversity, dominance concentration, life form, leaf size, leaf surface, leaf margin, evergreenness, vegetative reproduction, pollination, flower color, dissemination, polyploidy, and primary productivity.

Introduction

Spatial variations in climate tend to group species according to types of form and function that are of regional advantage. This is accomplished either by shaping the evolution of species that remain long in one region or by controlling the migration of others so that they are forced into environments most appropriate to the form and function as opportunities are presented. Adaptive characters can be identified by inference from correlations between types of climate and frequencies of characters that diverge from worldwide averages. Such inferences are then confirmed if similar correlations are found in different geographic areas having different floras. Such use of mass measurements yields conclusions that are either impossible or difficult to reach by experimentation.

Previous studies of the vegetation mosaic of eastern Washington and northern Idaho (Daubenmire and Daubenmire, 1968; Daubenmire, 1970) have been directed at recording the details of floristic composition and structure as related to climate, soils, fire, and grazing. The objetive here is to investigate systematically some salient features of plant structure and function that may possibly be adaptational along a climatic gradient transecting the same vegetation mosaic.

Knight (1965) analyzed grassland in Wisconsin with a similar objective, but he weighted species characters by their "prevalence," then fused all such analyses into a single "structural-functional index." Rather than follow this procedure I have considered the attributes separately, since such fusion always obscures fundamental differences. If attributes varied in unison, there would be little point in evaluating more than one of them. If they vary independently, information is lost in their fusion, for the same sum or "index" can be obtained from widely different combinations. Furthermore, at one end of the climatic gradient considered here drouth stress is of overriding importance (Daubenmire, 1968, 1972), whereas at the other end deficiencies of heat and nutrients have been found more critical (Daubenmire, 1956, 1970; Daubenmire and Daubenmire, 1968). There is no reason to suspect that any one plant character has the same ecologic significance throughout the climatic gradient. Should it ever be desirable, for a particular purpose, to calculate a "compositional index" for a segment of

this long climatic gradient, this can always be done if the details are presented separately, whereas interregional comparisons are impossible unless such an index is calculated in exactly the same manner. Since Knight's series was interpreted as being controlled only by moisture available in diverse habitats within a narrow range of macroclimates, his treatment did not have to take macroclimate into account.

General Methods

Floristic lists representing a series of plant associations along a climatic gradient are presented in two monographs (Daubenmire and Daubenmire, 1968; Daubenmire, 1970). All these lists refer to virgin stands in climax or near-climax condition, an interpretation that can be checked by referring to the details of community composition and population structure as published in those monographs. The few alien annuals that occurred in some of the stands at low altitude have been ignored here, and only those native species occurring in two or more of the tenth-meter plots in a stand were considered.

This restriction of consideration to communities that have approximated a steady state is a highly significant point, for it is well known that the weedy opportunists of disturbed communities differ materially in their structure and function from those plants which have been selected through centuries of competition as being best adapted to meet intense competitive stress in a given type of environment.

Among these associations only those are considered here that can be found on zonal soils, i.e., occuring as climatic climaxes. At each level along the climatic gradient there are other vegetation types, some being relatively warmer and drier types on thin soils or south-facing slopes, others relatively cooler and wetter types on north-facing slopes or stream terraces. Since the selection discriminated against these two types, each association in the catenary sequence represents a narrow segment of the climatic continuum bounded by regular and ecologically significant vegetation discontinuities. That these communities truly represent an unbroken series is attested by their ecotonal contacts in the field.

The purpose of the selectivity described above was to rigorously limit variables to a single one, i.e., climate, insofar as possible.

In the area of study, climatic gradients radiate in different directions from the center of maximum aridity, and since vegetation indicates the existence of qualitative differences along these different radii, a single radius was selected for consideration. Only those climatic climaxes were considered that occur along a line drawn from Vantage, Washington, eastward across Idaho to the crest of the Bitterroot Mountains. At the dry end of the catena, in the rain shadow of the Cascade Mountains, median annual precipitation is approximately 170 mm and mean annual temperature 11.2°C. At the crest of the Bitterroots annual precipitation is approximately 1000 mm and temperature 4°C.

For most analyses all stands representing this catena of associations were used, regardless of their distance from this line, on the assumption that environments must be equivalent where vegetation is closely similar.

At the dry end of the series, the stable vegetation of deep, well-drained loams and gentle slopes consists mainly of a layer of *Agropyron spicatum,* which covers approximately 40 percent of the ground, with a taller layer of *Artemisia tridentata* having at

most 20 percent coverage. This is referred to as the *Artemisia tridentata-Agropyron spicatum* association (Daubenmire, 1970).

As we move eastward, a position is reached where increasing moisture and decreasing temperature enhance moisture effectivity sufficiently for *Festuca idahoensis* to maintain a place in all stands, in addition to the *Artemisia* and *Agropyron*... This addition makes an easily observable marker of a biologically significant node along the climatic gradient, and the community is conveniently named the *Artemisia tridentata-Festuca idahoensis* association.

The next useful vegetation indicator of a still higher level along the moisture-temperature gradient consists of *Artemisia* losing its ability to maintain any representation on zonal soils. The mixture of *Agropyron* and *Festuca* that remains is referred to as the *Agropyron spicatum-Festuca idahoensis* association.

In a similar manner, the dropping out or addition of dominant components of any vegetation stratum has been used to divide the climatic continuum into segments that can be assumed to have a high order of ecologic significance, since the sequence is repeated so many places and since the vegetation within each belt shows little or no regular trend in its composition across the segment.

We have no way at present of ascertaining whether these vegetation-defined belts represent quantitatively equal segments of the climatic gradient, but it is probable that, on the average, this is true, since the same principles of vegetation classification have been followed consistently through steppe and forest. On the average about 40 percent of the species are shared between contiguous associations (Table 1), but, at two of the ecotones, floristic similarity is only half as great.

Each species was given a score for its characters, which was based on the author's long field-experience, supplemented by examination of herbarium specimens and taxonomic manuals. Where the scoring was equivocal, as in a species having both white-flowered and pink-flowered individuals, half a point was given each character.

TABLE 1. Coefficients of similarity (species shared as a percentage of the combined lists) between contiguous associations. This analysis is based on only six stands for each association, using the stands nearest the imaginary line described in the text.

Artemisia tridentata-Agropyron spicatum
48
Artemisia tridentata-Festuca idahoensis
48
Agropyron spicatum-Festuca idahoensis
24
Festuca idahoensis-Symphoricarpos albus
32
Pinus ponderosa-Symphoricarpos albus
30
Pseudotsuga menziesii-Physocarpus malvaceous
33
Abies grandis-Pachistima myrsinites
43
Thuja plicata-Pachistima myrsinites
45
Tsuga heterophylla-Pachistima myrsinites
57
Abies lasiocarpa-Pachistima myrsinites
20
Abies lasiocarpa-Menziesia ferruginea

Taxonomic Diversity

In the steppe monograph (Daubenmire, 1970) dominance data were based on 40 plots, 20 x 50 cm, in each stand. In the forest monograph (Daubenmire and Daubenmire, 1968) 50 such plots were used for undergrowth vegetation. In both studies the number of plots was considered to have exceeded the amount necessary to ensure relatively reproducible values for the analyses, and for that reason the difference in total area studied is ignored here for taxonomic diversity analyses.

In Table 2 the average number of species encountered in the series of plots in each stand is referred to as "species diversity," in the sense of floristic richness. There is a clear gradient with diversity at a maximum in the vicinity of the lower timberline, progressively fewer species being able to cope with increasing stress toward either warmer and drier, or colder and wetter, climates.

Since soil drouth is feeble in the *Abies grandis-Pachistima* belt and higher, but becomes progressively more severe down the series (although maximum diversity lies well down in the dry series), it may be concluded that the benefits of additional warmth outweigh the limitations of regular soil drouth (McMinn, 1952; Daubenmire, 1968a, 1972) in three of the phytoclimatic belts.

The strikingly abrupt impoverishment of the flora of the *Abies lasiocarpa-Menziesia* forest probably represents base deficiency in soils of the high ridges, magnifying the effect of progressive heat deficiency. There is no basis for suspecting a macroclimatic discontinuity at this ecotone. At the Priest River Experimental Forest in northern Idaho the thermal belt has been shown to lie between approximately 915 m and 1220m (Hayes, 1941), whereas the association in question lies above approximately 1433m (Daubenmire, 1973).

Another abrupt change in diversity occurs at the *Agropyron-Festuca—Festuca-Symphoricarpos* ecotone. It has been demonstrated that there is a difference in degree of soil drouth here, but the difference is no greater than at any other ecotone (Daubenmire, 1972). However, it is significant that this ecotone marks the boundary between lime accumulation and lime leaching, with the *Agropyron-Festuca* soils increasing in pH value with depth, and the *Festuca-Symphoricarpos* soils becoming slightly more acid with depth. Thus, neither of the two abrupt differences in floristic diversity seems relatable to moisture, but rather to soil chemistry, especially the base status of the soils.

It has been show previously (Daubenmire and Daubenmire, 1968) that when the seral as well as the climax tree species are considered for each habitat type, species diversity in the arborescent stratum is highest in the subalpine forests. But for the total flora, species diversity is highest at lower timberline (equally high in *Festuca-Symphoricarpos* and *Pinus-Symphoricarpos* associations). Thus, the diversity gradients for the different categories of life forms are distinctly different. In two other western mountain transects, total species diversity has been found to be highest well up in the forest sequence (Whittaker, 1965), rather than at lower timberline. Tidestrom (1925) concluded that in Utah and Nevada diversity is highest in the steppe (*Artemisia*) belt, decreasing progressively upward to the alpine summits and decreasing downward into the desert (*Larrea*) belt.

Species diversity as found in this study was not correlated with productivity, which is estimated to be highest in either the *Thuja-Pachistima* or *Tsuga-Pachistima* levels in the altitudinal sequence.

TABLE 2. Trends in vegetation characteristics through a series of plant associations representing a climatic gradient. Except for the first five horizontal arrays, the figures are percentages.

		Art-Agr	Art-Fes	Art-Fes	Fes-Sym	Pin-Sym	Pse-Phy	A.gr-Pac	Thu-Pac	Tsu-Pac	A.la-Pac	A.la-Men
N stands		15	6	11	19	8	13	16	11	19	14	14
N species in all stands		98	59	68	104	103	79	68	59	58	96	52
$\bar{x}$N species per stand (40-50 plots)		17	24	19	35	35	31	32	31	27	24	11
N multispecific genera per stand		0-4	5-6	0-3	0-3	0-3	0-3	0-3	0-4	0-4	0-4	0-2
Dominance concentration index		2.53	3.17	2.54	6.53	3.62	4.77	6.12	5.45	4.16	4.86	2.43
$\bar{x}$ Sums of coverage		127	144	157	282	105	135	87	104	58	108	139
Percentage of multispecific genera		12	19	5	6	4	3	5	4	6	7	11
Life form	Therophyte	27	31	22	13	7	5	1	1		1	
	Geophyte	17	19	18	21	24	23	19	16	22	18	12
	Hemicryptophyte	37	40	53	57	55	44	43	50	37	46	48
	Chamaephyte	12	10	5	5	3	7	13	15	18	13	15
	Nanophanerophyte	7	8	3	3	6	16	18	17	18	15	19
	Microphanerophyte				1	5	4	6	8	6	8	6
	Meso+Megaphanerophyte					1	1	1	1	1	1	1
	Liana								1		1	
Leaf size	Leptophyll	33	31	24	11	6	4			2	1	4
	Nanophyll	46	54	43	44	30	26	18	17	18	12	21
	Microphyll	19	14	28	40	51	55	63	60	53	59	62
	Mesophyll	1	2	5	5	6	15	19	23	25	23	12
	Macrophyll									2		
	Aphyllous	1		1							5	2
Glabrous leaf surfaces	Above	36	29	40	50	53	58	58	58	68	62	78
	Below	34	29	40	47	53	50	54	51	66	55	73
	Both sides	34	28	34	43	49	46	49	49	61	53	69
Entire leaf margins	All undergrowth	73	66	63	60	58	51	40	32	37	32	39
	Nano+Microphaner.	50	60	100	8	5	15	16	27	21	8	40

TABLE 2. (Cont.)

			Art-Agr	Art-Fes	Agr-Fes	Fes-Sym	Pin-Sym	Pse-Phy	A.gr-Pac	Thu-Pac	Tsu-Pac	A.la-Pac	A.la-Men
Evergreen leaves			7	4	10	8	14	16	34	29	37	19	29
Vegetatively spreading			5	2	16	21	21	36	53	52	56	44	45
Pollination	Insect		85	85	88	87	83	82	84	81	88	78	79
	Wind		13	15	12	13	16	16	15	9	6	14	15
	Water		1				1	1	1		6	8	6
Flower color	Red	22*	1			1						1	
	Pink-Magenta		10	8	11	14	11	10	11	6	7	13	7
	Dark purple	7				2	1	1		6	4	2	2
	Yellow	31	28	35	35	24	19	12	10	9	4	15	15
	Blue	1	10	9	13	14	17	11	4	4	2	7	4
	White	26.5	36	31	26	30	33	45	56	50	68	55	39
	Green	7.5	1	2	3	1	1	3	1	5	4	6	6
Dissemination	Wind	Plumose	20	28	31	19	11	11	4	5	2	14	12
		Minute	2	2	2		3	3	16	20	22	20	31
		Winged						1	1	1	2	1	4
		Tumbling	5	5	3								
		Catapult	28	29	28	40	32	23	13	10	8	22	13
	Animal	Fleshy+Aril	2		2	6	12	26	29	32	41	25	21
		Nut	1			1					2		
		Adhesive	8	6	2	3	5	7	9	10	10	8	2
		Explosive	3	2	6	10	9	5	7	5	6	4	4
	Unspecialized		30	28	28	21	29	23	19	15	8	6	13

* This and the figures directly below are the series of world-wide averages as computed by Weevers (1952).

Auclair and Goff (1971) found that average species diversity varied directly with average species constancy in east-central North America. This relationship was tested in the vegetation of eastern Washington and northern Idaho by considering the average numbers and average constancy of indigenous species encountered in the sets of sample plots in six stands of each association. There was not the slightest relationship.

The data in Table 2 show that in small stands of homogeneous vegetation distributed along the moisture-temperature gradient there is no trend in the actual numbers of genera with more than one species. However, since species diversity shows a decidedly curvilinear trend along the gradient, the percentage of genera with more than one species follows an inverse trend: the richer the flora, the smaller the proportion of genera with more than one species.

Elton (1946), using published lists for plant communities to calculate the percentage of genera with varying numbers of species, compared 27 communities representing a wide range from arctic tundra to temperate-zone forests. He found that 4 to 37 ($\bar{x} = 16$) percent of the genera in each community have more than one species. The average for the present region is considerably lower: 7.5 percent. The clear parabolic trend is inversely related to the trend in species diversity, but the significance of this is obscure.

In another geographic area, Stebbins (1972) found evidence that the number of species per genus is highest at the ecotone where forest meets steppe or desert, but the reverse is true in eastern Washington and Northern Idaho.

Dominance Concentration

Canopy coverage percentages for each species have been determined individually, then summed for the stand. Since short species commonly occur beneath tall and the canopies of the tall species often intermingle, the coverage sum for a stand commonly exceeds 100 percent. With the tree stratum ignored throughout, the minimum number of species required to provide 75 percent of the coverage sum for each stand has been determined and the numbers averaged for the stands representing each association (Table 2). The lower the value, the greater is the concentration of dominance in this index.

A significant degree of correlation exists between dominance concentration and species diversity (Fig. 1), suggesting that floristic attenuation reduces the variety of competitive stresses and leaves certain niches useful to only one or two species, which can therefore have large populations that confer dominance.

About the only other generalization that seems possible with respect to ecologic implications is that, among the communities free of overhead shade, dominance concentration is lowest in the wettest member, and, among the communities free of severe soil drouth, stress is lowest in the warmest member.

It is suspected that the irregular relationship of dominance concentration to altitude is mainly a matter of random occurrence in the flora of a few species with high competitive abilities that gain full expression in particular segments of the climatic gradient.

Life Forms

Most life-form analyses have utilized floristic lists for all the plants of a large area, indiscriminately mixing the components of climax and seral communities of a great

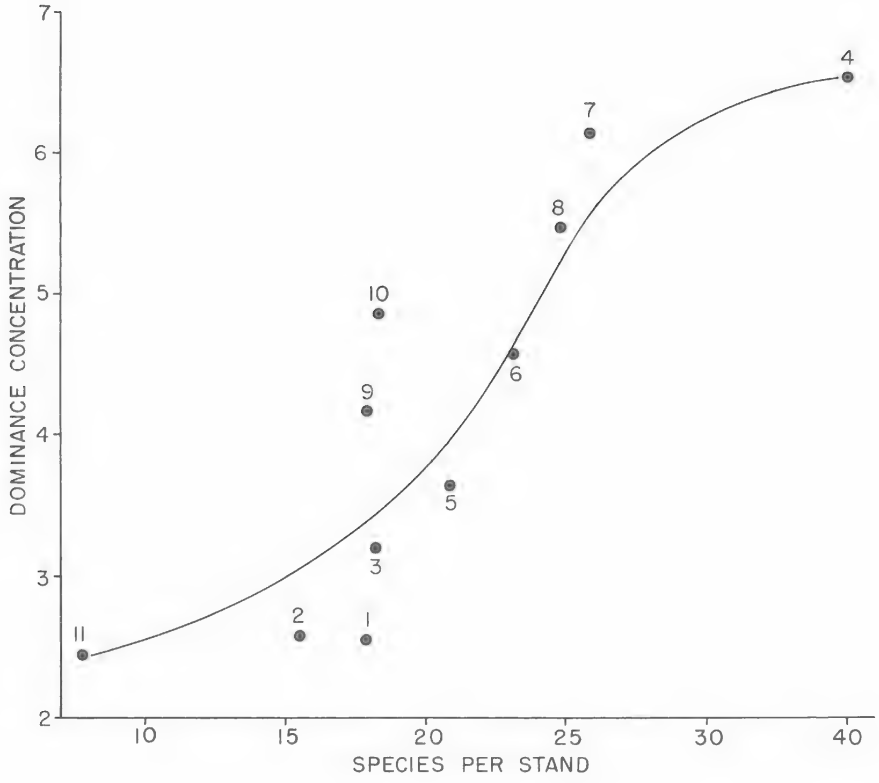


Figure 1. Relation of dominance concentration (minimum number of species to provide 75 percent of total coverage) to species diversity (number of indigenes in sample plots). The numbers refer to the relative positions of the associations along the climatic gradient from hot, dry (1) to cold, wet (11).

variety of xerophytic to hydrophytic habitat types. Restriction of consideration to just stable vegetation, and to just those types of stable vegetation that reflect climate most clearly, comes much closer to achieving the aims of life-form classification. Furthermore, only those elements of Raunkiaer's classification for which there is substantial evidence of adaptational value (Daubenmire, 1968b) have been employed.

Therophytes show the most perfect correlation between life form and the climatic gradient as a whole (Table 2), yet they show no clear trend toward further reduction in relative importance betyond that level on the moisture gradient (the *Pseudotsuga-Physocarpus—Abies grandis-Pachistima* ecotone) above which soils remain moist to near the surface throughout summer. Steiger (1930) found that only 10 percent of the fire-maintained grassland flora of eastern Nebraska was composed of annuals, a value well below that of any of the climatic grasslands included in the present analysis.

Geophytes tend to decline at either end of the moisture-temperature gradient; the decline as drouth intensifies, agreeing with Orshan's (1953) findings in Israel but not with Buell and Wilbur's (1948) data from Minnesota. Hemicryptophytes are well represented throughout and rather uniformly so. Chamaephytes are poorly represented in the vicinity of lower timberline, increasing toward both the dry and the cold extremes of climate. Orshan (1953) and Buell and Wilbur (1948) also reported a decrease in chamaephytes with reduced rainfall. Nanophanerophytes are most poorly represented in the two upper steppe zones, and in the forest they increase up to the subalpine zone. Microphanerophytes are almost restricted to forest but show no clear altitudinal trend.

The increase of chamaephytes toward the warm-dry end of the climatic gradient, as well as toward the cold-wet end, deserves comment. Raunkiaer considered chamaephytes as characteristic of high latitudes and altitudes, but among the data summarized by Cain (1950) one finds the chamaephyte percentages for hot steppe varying from 7 to 42 and for cold steppe from 3 to 23 percent. Thus, the degree of restriction of high chamaephyte percentages to high latitudes and altitudes is much less than Raunkiaer thought.

A number of workers have weighted life-form percentages with frequency data from plot studies in an attempt to make life-form spectra better reflect the physiognomy of the community. Buell and Wilbur (1948) made several comparisons of weighted and unweighted spectra, but the general character of their spectral pairs was similar in all but one comparison. They failed to note that frequency data are always strongly influenced by the size of sample plot used, so that the weighted values, like the frequency values, are not community parameters. It would seem that independent techniques of recording physiognomy (e.g., coverage values, profile diagrams, or photographs) are superior to weighted life forms. Hemicryptophytes may vary from tiny species with high frequencies, that contribute nothing toward determining physiognomy, to dominants 2m tall or more, that determine the physiognomy. Furthermore, life form is a measure of the degree and mode of adaptation to the least favorable season of the climate at a given location, whereas frequency and coverage are measures of ubiquity and success in competing with such ecologically equivalent species as are also adapted to the local climate. The two evaluations measure different attributes, and fusing simple statistics that describe different attributes nearly always buries information in a complex statistic that is difficult to interpret.

Since the hemicryptophyte class exceeds all others even in the driest part of eastern Washington, that area clearly does not merit consideration as "desert," for in the flora of true deserts therophytes clearly exceed hemicryptophytes. This conclusion is buttressed by the fact that at least half a ton of perennial grass is produced per acre per year on zonal soils in the dry climate of the *Artemisia-Agropyron* zone (Daubenmire, 1970).

Although alien species were seldom encountered in the virgin or near-virgin stands of the associations considered in this report, and were ignored in the previous paragraphs, their life forms and distribution through the sequence of communities are of special interest. No woody alien species were represented. Annuals were restricted to those associations in which the soil profile regularly dries to a considerable depth, and their altitudinal distribution among these associations tends to form a bell-shaped curve centered on *Agropyron-Festuca* association (Table 3). Perennial aliens were

almost as closely restricted to the warm-dry environments, but their best representation was in the *Pinus-Symphoricarpos* association. No aliens were ever encountered in the four coldest and wettest environments.

TABLE 3. Total number of alien species encountered in all stands studied. Often the species were represented by a single individual, but plants unable to develop past early seedling stages have been ignored.

Associations	Annuals	Perennnials
Artemisia tridentata-Agropyron	2	1
Artemisia tridentata-Festuca	10	2
Agropyron-Festuca	16	2
Festuca-Symphoricarpos	13	5
Pinus-Symphoricarpos	6	12
Pseudotsuga-Physocarpus	2	7
Abies grandis-Pachistima	0	6
Thuja-Pachistima	0	0
Tsuga-Pachistima	0	0
Abies lasiocarpa-Pachistima	0	0
Abies lasiocarpa-Menziesia	0	0

Obviously the alien element is tending to have a strong modifying influence on the life-form spectrum of the flora as a whole and is having very different influences in the different plant associations. Their distribution may possibly reflect a lower degree of niche saturation in the drier climates, but possibly it is only at low altitude that there has been sufficient disturbance for a long enough time to provide the required opportunities for establishment. However, *Bromus tectorum,* at least, has become a very minor member of communities in which there has been no possibility of any disturbance by man or livestock (Daubenmire, 1970).

Leaf Size

Average size of leaf, classified according to Raunkiaer's system, shows strong and consistent relation to the climatic gradient (Table 2). The two smallest size classes are best represented at the warm-dry end of the series, declining until they attain their poorest representation in forests characterized by the *Pachistima* type of undergrowth. Microphylls and mesophylls, taken together, show exactly reversed trend since the data represent percentages. A reversion toward size characteristic of dry climates is observable at the cold-wet terminus of the series.

Parkhurst and Loucks (1972) have devised a model based on an assumption that water-use efficiency is the key to optimal leaf size in any given environment. Their model agrees fairly well with the long-recognized fact that large leaves tend to be confined to ever-wet, warm, shady microclimates, whereas small leaves are characteristic of foliage exposed to either low temperatures or strong insulation. The tendencies observed in Table 2 agree perfectly with this concept, since there is a tendency toward microphylly in the coldest of the forest belts which might be expected to intensify if our mountains extended high enough to support an alpine tundra.

Leaf Surfaces

The character of leaf surface was based almost entirely on descriptions in taxonomic manuals. Scabrous and glabrate surfaces were lumped with glabrous, and when

pubescence was restricted to veins or leaf margins, it was ignored.

About one-third of the species have glabrous leaves in the driest part of the steppe, with the percentage increasing with altitude until about three-fourths are glabrous in the subalpine forests (Table 2). Although slightly more leaves are glabrous on the upper surface than below, the three types of statistics presented do not differ significantly.

If trichomes die as they mature, pubescence on the upper surface would serve to reduce the heat load on the blade below, as well as to thicken the boundary layer of still air. Both these influences would reduce cuticular transpiration. Hairs on the lower surface should be of significance principally in thickening the boundary layer, since in none of the associations is there reflection from a bare soil. With both types of functions presumably related to water economy, the trend from steppe to subalpine forest finds a rational interpretation as an adaptation. Thus, the independent trends in leaf-surface character and in life form agree in pointing to a progressive increase in moisture effectivity throughout the series of associations studied.

Leaf Margins

In tallying leaf margins attention was confined to the leaflet in compound leaves, and undulate margins were lumped with toothed, lobed and incised as "nonentire."

When all nonarboreal species are considered collectively, there is a gradual trend from a high percentage of entire leaves at the warm-dry end of the climatic gradient to a low percentage in the *Thuja-, Tsuga-* and *Abies lasiocarpa-Pachistima* forests. A slight upward trend of dubious significance is seen at the extreme upper end of the series, where an impoverished flora may have been somewhat inadequate to provide a highly reliable value. This trend is strikingly parallel to that of leaf size, with a strong correlation between microphylly and entire margins.

Paleobotanists have made much use of the well-known gradient in percentage of entire leaves in woody plants when attention is restricted to moist lowlands and a transect is considered from arctic to equatorial regions. It is generally stated that the leaf-margin character of herbs shows no corresponding relation to climate. Possibly this is simply a restatement of conclusions by Bailey and Sinnott (1915), who made the original classical study of leaf margins in relation to climate. With 60 to 93 percent of our subarboreal vegetation herbaceous (therophytes + geophytes + hemicryptophtyes), it was considered of interest to tally separately the medium to tall shrubs, since these are included in the woody floras that are considered in relating leaf margins to climate and which, in fact, constitute our entire representation of the category used by paleobotanists. The results for these woody species (Table 2) are quite erratic, so it is the strong trend among the herbaceous plants that produces the clear trend when the total flora is considered. Thus, the statement that the leaf margin of herbs bear no relation to climate is not borne out in this flora.

Evergreenness

Leaf duration is difficult to assess since a number of steppe species will remain green during the normal season of aestivation if the summer is unusually wet, whereas in the forest some will remain evergreen if an early snow persists and keeps them covered through winter. The intention has been to reflect average situations in the tallies.

In temperate latitudes evergreenness has attracted interest from diverse standpoints. In 1921 Rigg called attention to the high percentage of evergreen species in the vegetation of the Puget Sound area. His interest in this phenomenon centered on explaining the psysiology of leaves that enables them to endure periods of freezing weather in that area, and the low ratio of starch to sugar that develops in winter was emphasized.

Beatley (1956) compiled a list of herbs that retain green leaves through winter in Ohio and pointed out that about 20 percent of that state's herbaceous flora falls into this category. The adaptive significance of evergreenness was not an object of that survey.

Monk (1966) discussed local variations in the percentage of evergreen species in the flora of north-central Florida and hypothesized that their increasing representation on dry and infertile soil may indicate superior adaptation to retain nutrients against leaching loss.

Evergreenness is lowest in our hottest and driest climates (Table 2), increasing slowly as drouth stress decreases until that level is reached (the *Abies grandis-Pachistima* forest) where the stress of soil drouth has rather abruptly declined to a very low level. From here upward in the transect there is a relatively high proportion of evergreen species. The data show no significant trend within this moist series. If the few trees had been taken into consideration, the percentage for forest communities would have been raised, but by only a negligible fraction.

Along this transect evergreenness has a very different significance at low and high altitudes. The consistently low percentage in steppe probably reflects the difficulty of leafy plants in meeting transpiration stress during summers when the soils regularly dry to a considerable depth and there is no overhead canopy of tree foliage to ameliorate insolation with shade during a long season that is hot, cloudless, and rainless. It has been shown quantitatively that toward the dry end of the climatic spectrum more of our steppe plants have green foliage in midwinter than in the driest part of summer (Daubenmire 1970).

In the moist sector of the forest series drouth is a minor problem, but here the short annual supply of heat gives an advantage to species that can construct frost-hardy leaves capable of functioning during each brief spell of above-freezing weather in the relatively long spring and autumn seasons of our semioceanic climates.

Vegetative Reproduction

In this analysis only plants with rhizomes or runners that spread sufficiently to produce a sizable clone have been tallied as vegetatively reproducing. Also, the field behavior has been emphasized. *Achillea millefolium lanulosum,* for example, reproduces vegetatively only in disturbed areas where competition is minimal, whereas in the stable communities considered the individuals are very small and quite isolated.

Nearly half the species in the *Abies grandis-Pachistima, Thuja-Pachistima,* and *Tsuga-Pachistima* forests reproduce vegetatively (Table 2). The habit is only slightly less well represented in the colder subalpine forests above, but it decreases progressively downslope, becoming very poorly represented in the more arid steppe associations.

Since vegetative reproduction confers benefit by providing a new plant with a dependable supply of metabolites and water as long as needed for its establishment,

the value of this habit is easily seen in the dense shade of cool forest interiors where a combination of low temperature and limited light are undoubtedly obstacles to seedling establishment.

In the fire-maintained grassland of eastern Nebraska, Steiger (1930) found "the usual method of propagation is by vegetative parts." Assuming that this implies well over 50 percent of the species, a similar range of values is attained in my transect only above that ecotone will within the forest where the soils remain moist to near the surface throughout summer.

Pollination

In this analysis flower morphology has been the sole guide for judging the most effective pollinating agent, except for *Salix,* which is considered as insect pollinated. The movement of sperm to archegonium in the *Pteridophyta* has been taken as an environmentally equivalent hazard to the transfer of pollen from anther to stigma in seed plants.

No trends became evident in this analysis (Table 2) other than the dependence on water by ferns, which are restricted to the wetter end of the altitudinal spectrum. Since rainfall increases upslope and is essential for fern fertilization, the rationale for the altitudinal trend is obvious.

Nearly all woody plants that form the tallest vegetation layer, i.e., *Artemisia* in the two steppe associations and conifers in the forests, are exclusively wind pollinated.

Flower Color

Weevers (1952) analyzed whole floras representing widely separated parts of the earth. Ignoring anemophiles, as I have in the present study, he found that there is a remarkable consistency in the percentage distribution of the different flower colors of angiosperm corollas. His world-wide averages are included with results of the transect analyses in Table 2.

Along the transect the frequency of yellow flowers is essentially normal only in steppe, with distinctly low values in forest. In forest there is a parabolic trend of yellow values, dipping to only 14 percent of the world average in the very shady environment beneath *Tsuga heterophylla.*

Blue flower color tends to be the reciprocal of yellow in respect to its relation to the normal spectrum, for it is far above normal in steppe, approaching normal most closely in the *Tsuga* forest. White color, like yellow, approximates normalcy in steppe, rising to twice the expected value where undergrowth is consistently dominated by the *Pachistima* union. Green is far below normal except in the upper part of the forest series. The pink-magenta-red group is consistently below normal.

It is tempting to speculate that in the somber *Tsuga* forest white, which is strongly overrepresented there, would provide the greatest contrast with the dark foliage and moss-covered ground and thereby aid insects in locating flowers. However, such a conclusion makes the unwarranted assumption that insects perceive colors as man sees them. Yellow might seem fairly similar to white in its visual impact, yet this color becomes scarce in shady environments, and the twice-normal green flowers should logically be at a disadvantage against shaded greenery.

It is notable that the very highest or very lowest values for each color percentage

invariably fall in the forests that have the *Pachistima* type of undergrowth. Floristically this is a very rich type of undergrowth, and variations of color distribution within it might result from variations in the intensity of shade controlling species composition at different stages in the life history of the stands, some of which had not yet achieved complete stability. A study of light intensity in relation to variation color frequencies within this unit might be rewarding.

Major differences have shown up in comparing the data from this transect with Weevers' world-wide spectrum. White and especially blue are rather consistently better represented in eastern Washington and northern Idaho, so that all other colors are less well represented. A disconcerting aspect of this phenomenon is that we, as yet, have no clue as to the significance of flower color for the different pollinators. The facts that (1) there is a consistent difference in proportion of colors over the earth when whole floras are considered and (2) clear trends of differences occur along a single climatic gradient such as shown in Table 1 indicate that there are principles which have thus far eluded us.

Dissemination

Remarkably clear gradients are evident in disseminule types (Table 2). The tumbling type of wind-disseminated structure is confined to the driest part of the steppe where the dominant perennial grasses occur as well-spaced bunches. The still more widely spaced *Artemisia* bushes that rise to about a meter in height appear to be no deterrent to the success of this type of dissemination, for the tumblers are even less well represented where the same bunchgrasses extend beyond the limits of *Artemisia.* As alien weeds, tumblers are common on disturbed land in the *Festuca-Symphoricarpos* steppe, but in that belt there are no native species in this category.

The plumose type of anemochore is also best represented in the three driest types of steppe vegetation, with a rather progressive diminution evident through the higher associations, culminating in the very shady *Tsuga* forest. One might attribute this trend to less air movement in progressively thicker tree canopies, but for the curious increase in both *Abies lasiocarpa* associations where shade is only a little less dense.

Despite the wind-stilling influence of tall trees, both the winged and the minute types of anemochores increase progressively with altitude, with best representation in the *Abies-Menziesia* forest.

Disseminules with fleshy parts are poorly represented at the arid end of the transect, achieving their best representation in the Tsuga forest. The trend of this category is approximately the reciprocal of that of both the plumose type and the unspecialized type.

All plants that retain their disseminules on an erect inflorescence held above the foliage for an indefinite postmaturity period have been classed as the catapult type. Both the catapult and explosive categories are best represented in the vicinity of the forest-steppe ecotone.

Except for the tumbling type of disseminule, the clear trends described above find no ready interpretation as adaptations. Rather, they seem a consequence of taxonomic groups having particular disseminule types, with the groups restricted to different climates on the basis of other characters. To illustrate, 29 percent of the flora in the *Artemisia tridentata-Agropyron* association is *Compositae,* a family having

many species will plumose disseminules but no species in the small-seeded and small-spored groups *Ericaceae, Orchidaceae,* and *Polypodiaceae.*. On the other hand, in the *Tsuga* forest these values are nearly reversed: 4 percent in the *Compositae* and 31 percent in the *Ericaceae-Orchidaceae-Polypodiaceae* groups. The degree to which taxonomic groups are restricted to different segments of the climatic gradient is indicated in Table 4.

Logic seems treacherous as a basis for judging the importance of disseminule efficiency. For example, Faegri (1963) pointed out that the small, winged seed of *Pinus sylvestris* would seem adapted for much faster travel than the heavy nut of *Corylus,* but *Corylus* traveled the faster in post-Wisconsin range readjustments in Europe. Furthermore, logic would suggest that good evidence of the efficiency of a mode of dissemination would be the high presence (or constancy) of a species through the scattered stands of an association. The materials at hand provided an opportunity to test that hypothesis.

Three associations were selected for the test, representing low, intermediate, and high altitudes, and, considering only those disseminule types which were well represented, the mean percentage presence of the species in each type was determined. If the hypothesis were valid, one would expect plants with no apparent adaptation for dissemination to have lower presence than those of the catapult type, with plumose species most consistently present in the different stands of an association. Alternatively, unadapted disseminules, minute disseminules easily carried by wind, and berry fruits susceptible to long-distance transport by birds should be associated with progressively higher presence values.

The results (Table 5) indicate that the regularity of a species reappearance in areas of closely equivalent environment is quite unrelated to their dissemination efficiency as judged by morphology. Geographic distribution is undoubtedly determined by other factors as well as by mobility, and some of these factors could be of paramount importance for different species. For example, any species that may have entered our flora rather recently may still have limited distribution despite an apparently efficient dissemination system. On the other hand, isolated populations of a relictual species may have been suffering random local extinction, with dissemination efficiency unable to counteract the effects of a climate that has been growing less favorable.

Polyploidy

An attempt was made to compare the floras of the associations on the basis of the relative abundance of species with polyploidy reported, in contrast to those that appear strictly diploid. However, the requisite cytologic data are available for relatively few of the species, and it seemed advisable to combine the floras of the two highest and the two lowest associations to make lists roughly comparable with one association in approximately the middle of the climatic series. Even so, the results must be considered extremely tentative. Exactly half of all the species for which reports are available are strictly diploid, so deviations from this ratio in any segment of the flora may be significant.

Deviation is substantial only in the subalpine forest at the cold, wet end of the vegetation catena (Table 6). Thus, it would appear that polyploidy is advantageous under the stress of suboptimal heat but not under the stress of suboptimal moisture.

TABLE 4. Percentage distribution of the 20 best represented families by association. The order reflects major distributions shifting from the dry to the wet ends of the climatic range.

	Art-Agr	Art-Fes	Agr-Fes	Fes-Sym	Pin-Sym	Pse-Phy	A.g-Pac	Thu-Pac	Tsu-Pac	A.l-Pac	A.l-Men
Polygonaceae	3	3		1	1						
Polemoniaceae	6	8	4	5	2	1					
Boraginaceae	9	7	4	1	2	1	1				
Portulaccaceae		2	3	2	3	1	1	3			
Compositae	27	36	32	18	12	10	6	7	3	8	8
Leguminosae	9	7	12	11	7	5	3	2	1	1	2
Umbelliferae	6	3	4	3	6	3	1	3	1	2	
Gramineae	9	12	12	11	13	11	6	2	1	3	4
Scrophulariaceae	2	3	3	5	3	4		3		4	2
Caryophyllaceae	1		1	5	4	3	1	2		1	
Onagraceae	3	2	3	3		3	1	2	1	1	2
Saxifragaceae (s.l.)	2	2	1	3	5	5	6	5	3	6	6
Liliaceae	5	5	6	7	10	7	10	12	16	9	8
Ranunculaceae	3	3	4	3	2	3	10	10	5	8	6
Rosaceae	1		3	7	11	7	12	10	7	9	4
Cyperaceae				3	2	3	3	2	3	3	4
Caprifoliaceae				1	1	3	6	10	3	3	6
Ericaceae (s.l.)					1	4	13	10	17	12	28
Polypodiaceae					1	1	1	12	10	6	6
Orchidaceae					1		1	2	3	6	4

TABLE 5. Presence among the stands of an association as related to the types of disseminules.

Associations	Mean presence percentages and disseminules types		
Artemisia tridentata-Agropyron	33.5 nonadapted	36.2 catapult	31.5 plumose
Festuca idahoensis-Symphoricarpos	23.7 nonadapted	31.8 catapult	28.3 plumose
Thuja plicata-Pachistima	49.1 nonadapted	39.6 minute	50.7 berry

TABLE 6. Polyploid-diploid status of floras at three levels along the climatic gradient.

Source of lists	Size of list	Species considered	Percentages	
			Diploids	Polyploid
Artemisia tridentata-Agropyron + *Artemisia tridentata-Festuca*	52	25	52	48
Pinus ponderosa-Symphoricarpos	64	34	44	56
Abies lasiocarpa-Pachistima + *Abies lasiocarpa-Menziesia*	52	15	68	32

It has been hypothesized that vegetative reproduction is a means of conserving polyploidy that confers survival value in adverse habitats, thus offsetting the resultant difficulty of setting seeds abundantly. Therefore, polyploidy should be more associated with plants with effective means of vegetative spread than with others (Stebbins 1950). There is little in the data at hand to confirm this hypothesis since 23 percent of the diploid species reproduce vegetatively, with only a few more (30 percent) of the polyploid species capable of reproducing in this manner.

Productivity

Estimates of net primary productivity are available for three of the steppe associations considered in this altitudinal sequence and one additional association (Daubenmire 1970). These are based on the oven-dry weight of the terminal standing crop of shoots, with early- and late-developing species clipped at the time they approximated full shoot development. For shrubs only the current year's twig growth, plus leaves and inflorescences, were taken.

A trend of increasing productivity from the dry edge to the wet edge of the steppe is clearly evident in the data (Table 7). No comparable data for the forest members

TABLE 7. Terminal standing crop in virgin, ungrazed stands of steppe vegetation.

Association	$g/m^2/yr.$ oven-dry
Artemisia tridentata-Agropyron spicatum	82.6 103.6 115.0
Agropyron spicatum-Festuca idahoensis	147.1 253.0
Festuca idahoensis-Symphoricarpos albus	296.0 368.0

of the series are available, but since average basal area increases to a maximum in the *Thuja-Pachistima* and *Tsuga-Pachistima* forests and then declines above (Daubenmire and Daubenmire, 1968), it is suspected that productivity likewise will prove to culminate in those two associations.

In addition to the substantial correlation of productivity with moisture balance, there is a slight tendency toward correlation with species diversity and with dominance concentration (Table 8).

TABLE 8. Relationships among productivity, species diversity and dominance concentration among stands of climax vegetation. Species diversity refers to the number of species encountered in samples of standard size. Dominance concentration refers to the fewest number of species required to provide 75 percent of the sum of coverages of all species in the stand.

Association	Stand Number*	Grams m^{-2}	Species Diversity	Dominance Concentration
Artemisia tridentata-Agropyron spicatum	27	71.9	17	3
"	10	82.6	14	2
"	42	103.6	15	3
"	40	115.0	—	–
Agropyron spicatum-Poa sandbergii	56	125.7	13	2
Agropyron spicatum-Festuca idahoensis	60	147.1	16	2
Artemisia tripartita-Festuca idahoensis	62	144.2	36	5
Festuca idahoensis-Symphoricarpos albus	155	368.0	40	6

* Other data for these stands are available, by number, in Daubenmire (1970).

Discussion

The vegetation catena that has been analyzed shows clearly that climate has either influenced the evolution of the species which have long been members of this flora or has determined the position along the climatic gradient which each had to take in order to enter the region. With evolution being such a slow process in plants, control over the position of immigrants in the landscape has probably been the major type of control that has operated.

Both structural and functional characteristics have been involved in determining the climate which most species have found most hospitable. Few attributes show a linear trend throughout; most are parabolic, suggesting that extreme warm-dry and cold-wet environments place a premium on different attributes. Plants are best adapted to warm-dry environments if they are diploid annuals with small, hairy, entire leaves that are deciduous and have disseminules that are plumose, if specialized at all. Those adapted to cold-wet climates are perennials, commonly polyploids, reproducing vegetatively, often woody, with leaves that are relatively large, glabrous, nonentire, and often evergreen. Evidence of drouth stress at low elevation and cold stress at high, with relatively favorable environment for vascular plants more centrally located, is shown by a reduction in primary productivity at both ends of the transect and by the attenuation of species diversity at the extremes, which probably reduces the variety of competition stresses so that dominance can be concentrated in the few species.

Literature Cited

Auclair, A. N., and F. G. Goff. 1971. Diversity relations of upland forests in the western Great Lakes area. Am. Nat. 105:499-528.

Bailey, E. W., and I. W. Sinnott. 1915. A botanical index of Cretaceous and Tertiary climates. Science 41:831-834.
Beatley, J. C. 1956. The winter-green herbaceous flowering plants of Ohio. Ohio J. Sci. 56:349-377.
Buell, M. F., and R. L. Wilbur. 1948. Life-form spectra of the hardwood forests of the Itasca Park region, Minnesota. Ecology 29:352-359.
Cain, S. A. 1950. Life-forms and phytoclimate. Bot. Rev. 16:1-32.
Daubenmire, R. 1956. Climate as a determinant of vegetation distribution in eastern Washington and northern Idaho. Ecol. Mono. 26:131-154.
————. 1968a. Soil moisture in relation to vegetation distribution in the mountains of northern Idaho. Ecology 49:431-438.
————. 1968b. Plant communities. Harper & Row, New York. pp. 300.
————. 1970. Steppe vegetation of Washington. Wash. Agric. Exp. Sta. Tech. Bull. 62. pp. 131.
————. 1972. Annual cycles of soil moisture and temperature as related to grass development in the steppe of eastern Washington. Ecology 53: 419-424.
————. 1973. A comparison of approaches to the mapping of forest land for intensive management. For. Chron. 49:87-91.
———— and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Exp. Sta. Tech. Bull. 60. pp. 104.
Elton, C. 1946. Competition and the structure of ecological communities. J. Animal Ecol. 15:54-68.
Faegri, K. 1963. Problems of immigration and dispersal of the Scandinavian flora. *In* North Atlantic biota and their history. Edited by A. Löve and D. Löve. Pergamon Press, N. Y. pp. 221-232.
Hayes, G. L. 1941. Influence of altitude and aspect on daily variations in factors of forest fire danger. U.S. Dep. Agric., Cir. 591. Washington, D.C.
Knight, D. H. 1965. A gradient analysis of Wisconsin prairie vegetation on the basis of plant structure and function. Ecology 46:744-747.
McMinn, R. G. 1952. The role of soil drought in the distribution of vegetation in the northern Rocky Mountains. Ecology 33:1-15.
Monk, C. O. 1966. An ecological significance of evergreenness. Ecology 47:504-505.
Orshan, G. 1953. Note on the application of Raunkiaer's system of life forms in arid regions. Palestine J. Bot. (J. Ser.) 6:120-122.
Parkhurst, D. F., and O. L. Loucks. 1972. Optimal leaf size in relation to environment. J. Ecol. 60:505-537.
Rigg, G. B. 1921. Some factors in evergreenness in the Puget Sound region. Ecology 2:37-46.
Stebbens, G. L. 1950. Variation and evolution in plants. Columbia Univ. Press, N. Y. pp. 643.
————. 1972. Ecological distribution of centers of major adaptive radiation in angiosperms. *In* Taxonomy, Phytogeography and Evolution. Edited by D. H. Valentine. Academic Press, N. Y. pp. 7-34.
Steiger, T. L. 1930. Structure of prairie vegetation. Ecology 11:170-217.
Tidestrom, I. 1925. Flora of Utah and Nevada. U.S. Nat. Herb., Contrib. 25. pp. 665.
Weevers, T. 1952. Flower colours and their frequency. Acta Bot. Neerl. 1:81-92.
Whittaker, R. H. 1965. Dominance and diversity in land plant communities. Science 147: 250-260.

Received January 9, 1975.
Accepted for publication March 11, 1975.

Joy Belsky

Department of Botany
University of Washington
Seattle, Washington

An Oil Spill in an Alpine Habitat

Abstract

A study was made of the vegetational damage caused by a spill of 7,000 gal of diesel fuel into an alpine meadow near Mt. Baker, Washington. Most of the herbaceous plants in the *Carex nigricans* and *Phyllodoce empetriformis-Cassiope mertensiana* associations were killed; the woody species were severely damaged but survived the effects of the oil. The root systems of the plants escaped major damage, possibly due to the oil flowing over the water-saturated soil surface. One year later, *Carex nigricans, Carex lenticularis,* and various mosses were invading the area.

During the past few years, periodicals have described environmental damage caused by crude-oil spills in the ocean. Dead fish, oil-soaked birds, economic losses, and despoiled recreational facilities have dramatized the ecological situation and initiated many investigations into oil in the marine environment. However, little is known about the effects of crude or refined oil on terrestrial ecosystems, particularly on extreme environments such as alpine meadows. Therefore, when a spill of diesel fuel occurred on an alpine meadow near Mt. Baker in northwestern Washington on U.S. Forest Service land leased by the University of Washington, I became interested in studying the effects of the oil on the vegetation. Such a study has special relevance in view of the Trans-Alaska Pipeline now being built. Spills of crude oil during drilling in and transport over the Alaskan arctic tundra can be envisioned; thus the potential for environmental damage must be evaluated. Also, the increased construction of alpine-zone recreational facilities presents a hazard to high elevation communities from heating-oil spills. Alpine and arctic tundra areas are, in many respects, similar, fragile ecosystems; long, cold winters and short growing seasons lead to slow soil development and decomposition of organic materials, to slow plant growth and regeneration, and to decreased plant diversity. The arctic and alpine ecosystems, however, differ in other important aspects (Billings, 1973).

Descriptions of damage and regrowth of an alpine meadow after an accidental spill of refined oil will be useful in planning for alpine and arctic tundra facilities and for rehabilitation of plant communities after oil spills.

Background

During March and early April, 1972, and oil spill occurred at the Cascade Field Station (the former Austen Pass Warming Hut) at an elevation of 1,330 m, near the terminus of Washington State Highway 542 on Mt. Baker, Washington. Approximately 7,000 gal of No. 2 diesel fuel slowly leaked out of storage tanks adjacent to the station when they were crushed by a heavy snow pack. Over a period of several months, the fuel (SSU Viscosity = 35 at 122° compared to SSU = 170 for crude oil) percolated through a snow-water mixture which was under 10 m of snow. The fuel slowly flowed down a hill and drained into Bagley Lake (elevation, 1262 m).

I visited the area immediately after the snow had melted in mid-September, 1972. Damage to the vegetation was confined to three areas: (1) the basin adjacent to the hut, (2) a wet sedge meadow 10 m below, and (3) a 0.3-0.6-m-deep water course, which dissects the meadow and empties into the former Bagley Lake. The effect of the oil on Bagley Lake was not investigated since this manmade lake has been allowed to drain. Figure 1 is a sketch map of the area showing the regions of damage.

Three areas of inquiry were suggested by this unique situation, a fresh oil spill on an alpine community: (1) what is the influence of diesel fuel on alpine plants and communities, (2) how does succession proceed in an alpine community after a seemingly severe perturbation by diesel fuel, and (3) what sound ecological techniques can be used to rehabilitate the meadow? This paper addresses the first question and describes the initial stages of succession. Succession and rehabilitation will be the subjects of a subsequent paper.

Description of Study Site, 1972

When the snow melted from the meadow in September, 1972, the area smelled of diesel fuel and an oil sheen was seen on all standing water. The nature of the damage visible at this time was particularly interesting. Although all the vegetation showed oil damage and, at first inspection, was completely brown or black, most plants retained small patches of green, living tissue distributed randomly throughout the otherwise brown plants.

The alpine meadow partially damaged by the oil is a mosaic of alpine plant communities which seem to be distributed along gradients of moisture associated with

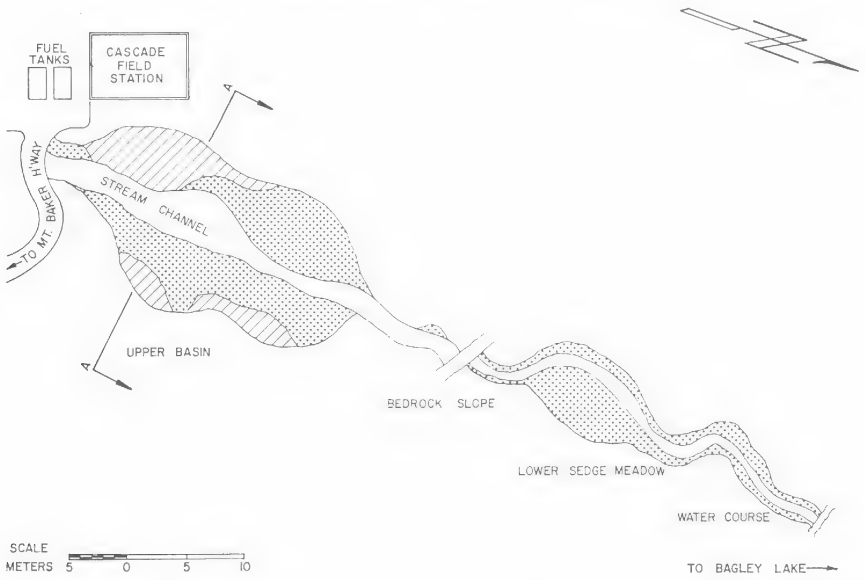


Figure 1. Sketch map of oil-damaged alpine communities, Cascade Field Station, Mt. Baker National Forest, Washington. Dots indicate *Carex nigricans* association; stripes indicate *Phyllodoce empetriformis* association.

topography. The shallow residual soil is underlain by columnar basalt, and there are bare areas of rock and gravel in the channel. The original associations were described using a series of quadrats distributed on undisturbed portions of the meadow. Nomenclature for all species of vascular plants follows Hitchcock *et. al.* (1973); nomenclature for mosses follows Lawton (1971).

A *Carex nigricans* association (Douglas, 1971) covers the flat, wet parts of the meadow. Based on 20 0.1-m^2 quadrats, *C. nigricans* shows a mean of 79±20 percent cover and a frequency of 100 percent. A small amount of *Juncus mertensiana* is present in very wet depressions, and *Carex lenticularis* var. *lenticularis* is locally present along the banks of the channel. Moss, lichens, and bare patches occupy the remaining spaces.

On better-drained, sloping ground a few centimeters above the *Carex* community, the sedge is abruptly replaced by a *Phyllodoce empetriformis-Cassiope mertensiana* association (Douglas, 1971) dominated by these species and *Luetkea pectinata.* The constituents of the *P. empetriformis-C. mertensiana* association are derived from ten 1.0-m^2 quadrats distributed on undisturbed portions of the better-drained meadow and are described in Table 1.

TABLE 1. *Phyllodoce empetriformis-Cassiope mertensiana* association surrounding impacted area.

	Cover (%)	Frequency (%)
Cassiope mertensiana	32±30	60
Phyllodoce empetriformis	25±20	70
Luetkea pectinata	23±20	90
Carex nigricans	18±30	60
Carex sp.	4±12	40
Vaccinium deliciosum	3± 4	60
Tsuga mertensiana	2± 4	30
Deschampsia sp.	trace	50
Hieraceum sp.	trace	60
Mimulus lewisii	trace	10
Juncus martensiana	trace	10
Saxifraga ferruginea	trace	10

The basin adjacent to the station received the greatest penetration by the oil, with 290 m^2 of vegetation being damaged. The original distribution of the vegetation can be reconstructed on the basis of observations in the immediate vicinity and at the margins of destruction (Fig. 2). The moss, *Rhacomitrium sudeticum* var. *alpinum,* and the herbs, *Saxifraga ferruginea, Luetkea pectinata,* and *Hieraceum* sp., seemed to be completely killed by the oil. However, the woody heathers, *C. mertensiana* and *P. empetriformis,* and the mountain hemlock, *Tsuga mertensiana,* retained some undamaged green leaves arranged in random 1-2-cm^2 patches throughout the oil-killed, brown leaves. The plants were usually 85-95 percent brown. Although plants in the lowest part of the basin were completely dead, most *Carex nigricans* individuals retained oily-green leaf bases which persisted throughout the first growing season.

In the lower wet meadows, large patches of *C. nigricans* were damaged where the water course had flooded its channels during snow-melt. The vegetation on a 0.2-0.3-m strip along the entire length of the course was also damaged by oil overflowing the banks.

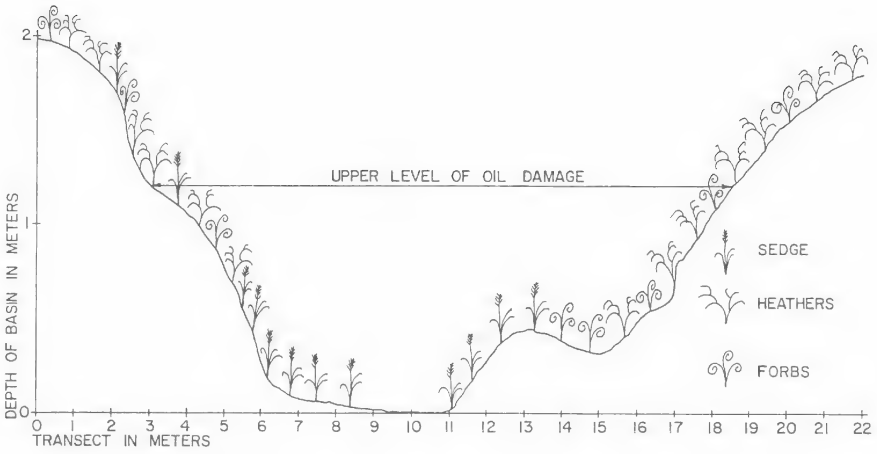

UPPER LEVEL OF OIL DAMAGE
SEDGE
HEATHERS
FORBS
DEPTH OF BASIN IN METERS
TRANSECT IN METERS
0
1
2
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22

Figure 2. Cross-section and vegetational cover of upper basin along Transect A noted in Figure 1. Upper level of oil damage is indicated by arrow. "Sedge" refers to *Carex nigricans* and *Carex* spp.; "heathers" refer to *Cassiope mertensiana* and *Phyllodoce empetriformis;* and "forbs" refer to *Luetkea pectinata, Vaccinium deliciosum, Hieraceum* sp., *Mimulus lewisii, Saxifraga ferruginea,* etc.

Recovery, 1973 and 1974

I visited the site several times during late summer, 1973, two growing seasons after the spill. Though the area was still superficially brown and the oil smell and the layer on the water still detectable, there was evidence of regrowth with some changes in vegetational composition.

The *Tsuga mertensiana* and most of the *C. mertensiana* had lost the rest of their leaves and had died, but the *P. empetriformis* and a few *C. mertensiana* individuals were forming profuse terminal and lateral buds. The few remaining green leaves from the preceding summer had died, so the plants consisted of stem and new growth. The *C. nigricans* in all areas seemed dead, the green centers being gone, but there were a few seedlings or sprouts of the sedge appearing in the otherwise dead sedge mat and in oil-covered muddy areas in the lower meadow. No new herbaceous plants were invading the area; but the *Rhacomitrium* was beginning to grow throughout and, by the end of the summer, was forming green mats. Along the damaged part of the water course the bright green sedge, *C. lenticularis,* was growing vigorously. It seems to be much more tolerant of the oily soil than is the *C. nigricans.*

In 1974, the disturbed meadows were covered by an unusually deep snow pack until late September. In spite of the extremely short growing season, the successional trends seen the year before were continuing. The heathers developed a second year's growth of leaves; and patches of *Rhacomitrium,* sometimes a decimeter in diameter, seemed to be growing vigorously and forming a new, green ground cover. New plants of *C. nigricans* were growing through the dead mat, and *C. lenticularis* was growing profusely along the stream bank.

Discussion and Conclusion

Continued observations in the field and a review of literature on the effects of oil on plants have given sufficient information concerning the function of the plants and

the system to suggest hypotheses about the differential damage to the plants in the upper basin. The oil seeped from the storage tanks into the snow and migrated horizontally on ice lenses in the snow as well as vertically to the ground. This flow outward in the snow might account for the intermittent damage to the plants up to 1.5 m above the bottom of the basin. Horizontal oil seepage, plus the possibility that ice might have been frozen on the leaves, allowed random patches of leaves to escape damage. Under the snow, the soil was probably saturated with water. The bulk of the 7,000 gal of diesel fuel, therefore, flowed over the soil surface and down the hill. Wein and Bliss (1973) found that the lightweight oil did not penetrate permafrost layers or the water table and that roots within these saturaed layers were protected from damage. This might account in part for the minimal damage to soil fertility and to root systems. Some of the oil probably penetrated the soil, but the melt-water from 10.0 m of snow plus that from higher ground would have leached out most of it. After the snow melted, any remaining lighter oil fractions would have evaporated. According to Wein and Bliss (1973), in Alaska the summer evaporation rate of crude oil is from 28 percent to 36 percent as measured with a miniature evaporimeter.

There are indications that the root anatomy itself guards the plant from oil damage. Unlike the lipophilic cuticle and stomatal openings covering the aerial parts of terrestrial plants, the roots have no stomatal openings and are surrounded by soil water. Though some crude oil fractions are water soluble (Baker, 1970), distilled petroleum components are generally insoluble (McCown, Brown, and Murrman, 1971). In any case, roots seem to be less sensitive to oil than are stems and leaves (Baker, 1970).

The few records of oil spills or experimental oil applications on terrestrial plant communities indicate that stems which are thick or woody are protected from oil damage. Baker (1971) found that, in salt marsh communities, perennials received less damage from crude oil than did annuals. In the arctic, dwarf shrubs showed greater recovery from various levels of oil application than did mosses and herbs (Wein and Bliss, 1973). Inspection of spills made along the Haines-Fairbanks Military Pipeline in Alaska (Rickard and Deneke, 1972) show that only woody plants, if any, survived crude oil spills.

My observations agree with these reports. The woody stems of *P. empetriformis, C. mertensiana,* and *Tsuga mertensiana* survived the first year, while the herbaceous plants did not. *P. empetriformis,* which has twice the stem diameter of *C. mertensiana,* is more resistant to the oil and survived to the second growing season in greater numbers. The thick, woody stems of the heathers and mountain hemlock must protect the vascular systems of these plants. I can only speculate as to why *C. mertensiana* and *T. mertensiana* died during the second winter, while *P. empetriformis* survived. *P. empetriformis* may have more storage materials in its roots and stems. The plants must have had a negative net productivity during 1972 due to their vastly reduced photosynthetic surface. The *C. mertensiana* and *T. mertensiana* may simply have 'starved.' Or perhaps the meristematic tissues of the *P. empetriformis* stayed intact while those of the other two plants were destroyed and could put on no new growth.

Finally, the seemingly increased fertility of the soil in 1973, seen in the growth of the sedges and moss, might be attributed to: (1) continued cycles of snow-melt and leaching, (2) an increase in the soil's organic matter content from the oil-killed

vegetation, and (3) the activity of microbes which can decompose hydrocarbons. Work by Plice (1948) and Adams and Ellis (1960) shows that the number of soil microbes increases dramatically when crude oil or natural gas is added to the soil. This increase of microflora results in an increase in nitrogen and organic carbon in the soil. In Barrow, Alaska, McCown and Benoit (1970) found that five liters of crude oil/m^2 caused a two-to-three-fold increase in bacterial numbers. A similar increase was recorded by Bliss *et al.* (1973) in the arctic tundra.

It is still too early to make any statements concerning secondary succession in an alpine meadow after an oil spill. The only vegetative recovery thus far is by the heathers, *P. empetriformis* and *C. mertensiana,* by the carexes, *C. nigricans* and *C. lenticularis,* and by the moss, *Rhacomitrium sudeticum.*. This study is continuing.

With increased building of recreational facilities in temperate alpine areas and with construction of oil wells and pipelines in the arctic, the incidence of refined- and crude-oil spills in alpine and arctic tundra will probably become more frequent in the future. The results from this study at Mt. Baker are encouraging in that they suggest that the impact of spills of refined oil might be of shorter duration that has commonly been predicted.

Acknowledgements

I would like to thank Dr. R. B. Walker and Charles Nuss for introducing me to the problem and for supporting my efforts. Special thanks go to Dr. Roger del Moral and Ron Shrigley for help in the field.

Literature Cited

Adams, R. S., Jr., and R. Ellis, Jr. 1960. Some physical and chemical changes in the soil brought about by saturation with natural gas. Soil. Sci. Soc. Am., Proc. 24: 41-44.
Baker, J. M. 1970. The effects of oils on plants. Environ. Pollut. 1: 27-44.
Baker, J. M. 1971. Seasonal effects of oil pollution in salt marsh vegetation. Oikos 22: 106-110.
Billings, W. D. 1973. Arctic and alpine vegetations: similarities, differences and susceptibility to disturbances. Biosci. 23: 697-704.
Bliss, L. C., G. M. Cousten, D. C. Pattie, R. P. Resive, D. W. A. Whitfield, P. Widden. 1973. Arctic tundra ecosystems. Ann. Rev. Ecol. and Syst. Vol. 4: 359-399.
Douglas, W. 1971. The alpine-subalpine flora of the North Cascade Range, Washington. Wasmann J. Bio. 29: 129-168.
Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, Wa.
Lawton, E. 1971. Moss Flora of the Pacific Northwest. Hattori Botanical Laboratory, Japan.
McCown, B. H., R. J. Benoit, and P. Murrman. 1970. Oil ecology. *In* J. Brown and G. C. West (eds.), Tundra Biome Research in Alaska, U.S. IBP Report 70-1, p. 74-86.
McCown, B. H., J. Brown, R. P. Murrman. 1971. Effect of Oil Seepage and Spills in the Ecology and Biochemistry of Cold Dominated Environments. Ann. Rept. U.S. Army, CRREL, Hanover, N.H. 18 pp.
Plice, M. J. 1948. Some effects of crude petroleum on soil fertility. Soil Sci. Soc. Am., Proc. 13: 413-416.
Rickard, W. E., and F. Deneke. 1972. Preliminary Investigations of Petroleum Spillage, Haines-Fairbanks Military Pipeline, Alaska. U.S. Army CRREL, Hanover, N.H.
Wein, R. W., and L. C. Bliss. 1973. Experimental crude oil spills in arctic plant communities. British Ecol. Soc. 10: 671-682.

Received February 10, 1975.
Accepted for publication April 7, 1975.

W. H. Rickard

Ecosystems Department, Battelle Northwest
P. O. Box 999
Richland, Washington

Vegetation of Knob and Kettle Topography in South-Central Washington

Abstract

Vegetational analyses consisting of ocular estimates of frequency-of-occurrence canopy-cover and aboveground harvest by species were conducted during the spring of 1974 on knob and kettle topography in Benton County, Washington. The important vascular species were sandberg bluegrass, *Poa sandbergii,* and cheatgrass, *Bromus tectorum.* Net primary productivity was estimated at 175 g/m^2 and varied according to topographic position with swales three times more productive than ridges.

As the microtopography changed from gently undulating to steep, more plant species were encountered. Steep south-facing slopes had less canopy-cover and fewer species than steep north-facing slopes. South-facing slopes were dominated by cheatgrass while north-facing slopes were dominated by sandberg bluegrass.

Introduction

The most comprehensive descriptions of steppe vegetation in Washington State are those of Daubenmire (1970). These provide data on species composition and canopy-coverage in remnant stands of steppe vegetation in pristine condition. This study describes vegetation occupying a small acreage of knob and kettle topography located in the climatically hottest and driest part of south-central Washington. One other study describing vegetative features of knob and kettle topography in the non-forest region of the Pacific Northwest was conducted by Blinn and Habeck (1967).

The Site

Knob and kettle topography occupies about 600 acres adjacent to the south bank of the Columbia River in Benton County, Washington, Township 14N, Range 26E, Sections 21, 22, 27 and 28 at an elevation approximately 400 feet above mean sea level. Knobs consist of a thin veneer of fine-textured soil mixed with large amounts of river-washed gravels, cobbles, and boulders. The knobs rise 15-20 feet higher than the swales or kettles (Fig. 1).

The regional climate as recorded at the Hanford Meteorological Station located eight miles south shows annual precipitation amounting to slightly less than seven inches, with most of it occurring during late autumn and winter (Table 1). The summer months of July, August, and September are characteristically hot and dry.

The site probably was grazed by herds of sheep and cattle more or less continuously from 1870 to 1940, mostly in winter and early spring. The site and thousands of surrounding acres were incorporated into the government-owned Hanford Works Reservation in the early 1940's and grazing by livestock was terminated. For 30 years vegetation use has been confined to fall and winter grazing by small herds of mule deer (*Odocoileus heminomus*), flocks of Canada geese (*Branta canadensis*), and populations of seed-eating pocket mice (*Perognathus parvus*).

Figure 1. Ground-level photograph of knob and kettle topography.

TABLE 1. Mean monthly temperatures and total precipitation averaged over the period 1941-1972 from the Hanford Meteorological Station (modified from Stone *et al.* 1972).

Month		Temperature (°F)	Precipitation (Inches)	
Oct.	Plant Growing Season	53.0	0.61	
Nov.		40.2	0.80	
Dec.		33.1	0.81	
Jan.		29.4	0.97	Total 5.12
Feb.		37.4	0.58	
Mar.		44.2	0.38	
Apr.		52.5	0.44	
May		61.7	0.53	
June		69.2	0.70	
July		76.6	0.15	
Aug.		74.6	0.21	
Sept.		66.2	0.30	
Annual		53.2	6.84	

The presence of scattered, fire-blackened stumps of sagebrush indicates that sometime in the past the site supported at least some sagebrush plants.

Methods

Vegetational analysis was accomplished using the canopy-coverage, ocular estimation procedures of Daubenmire (1959) during the spring of 1974. One study line 50 meters long, established on more or less level terrain, was examined by observing 50, 2 x 5 dm plots spaced systematically at one-meter intervals along the line. In addition, five plots located along a broad ridge-crest habitat were hand harvested of the current season's plant growth, dried at 60°C, and weighed. These five samples were compared with five other plots randomly located in an adjacent swale habitat. To provide an objective assessment of species composition and amount of canopy-cover on contrasting steep, north-facing slopes and south-facing slopes, twenty-five plots were examined from the crest of a representative mound to the base on the north-facing slope, and the same number of plots were examined on the south-facing slope.

Results

A summarization of vegetational analysis conducted on gently undulating terrain is shown in Table 2. Grasses provided most of the ground cover, especially sandberg bluegrass, *Poa sandbergii,* and cheatgrass, *Bromus tectorum.* These were ubiquitous,

TABLE 2. Species composition, canopy-cover and frequency of vascular plants on gently undulating topography, May, 1974.

Species	% Frequency	% Cover
Bromus tectorum	100	39
Poa sandbergii	100	17
Microsteris gracilis	48	1
Sisymbrium altissimum	16	2
Draba verna	28	0.7
Descurainea pinnata	48	1
*Salsola kalii**	48	1
Total cover %	—	62

* Seedlings

occurring in every plot examined. Most of the forbs associated with the grasses were annuals. Clearly, grasses were the important contributors to aboveground live biomass with swales three times more productive than ridges (Table 3). It was calculated that

TABLE 3. Average dry weight (grams per one-tenth m^2 ± standard error) of plants harvested from ridge and swale habitats, May, 1974.

Species	Ridge	Swale
Bromus tectorum	7.1 ± 0.31	18.3 ± 3.2
Poa sandbergii	.75 ± 0.14	4.9 ± 1.2
Sisymbrium altissimum	0	2.1 ± 0.98
Descurainia pinnata	0	2.0 ± 0.87
Microsteris gracilis	0	0.1 ± 0.08
Calochortus macarocrpus	0	Trace
Plantago patagonica	0	Trace
	7.8	27.4

ridge sites produced an average of 80 g/m^2 while swales averaged about 270 g/m^2. Assuming that the landscape is about equally comprised of ridges and swales, an average of 175 g/m^2 can be derived.

The 1974 growing season (October-May) was marked by unusually favorable precipitation, 8.95 inches, resulting in luxurient plant growth. The yields are in the range of those reported for cheatgrass communities elsewhere on the Hanford Reservation (Cline and Rickard, 1973).

Species composition was enriched by steep microtopography (Table 4). Clearly,

TABLE 4. Comparison of frequency and canopy-cover for vascular plants on steep contrasting north- and south-facing slopes.

	% Cover		% Frequency	
Species	South	North	South	North
Bromus tectorum	24	13	100	96
[P]*Poa sandbergii*	0.9	34	16	100
Amsinckia lycopsoides	0	10	0	40
[P]*Delphinium* sp.	0	2	0	20
Microsteris gracilis	3	0.6	68	24
Draba verna	7	0.3	92	12
Descurainia pinnata	0.2	1	8	36
[P]*Phlox longifolia*	0	2	0	28
Cryptantha pterocarya	0.4	0	16	0
Gilia minutiflora	0.2	0.1	8	4
[P]*Allium* sp.	0.1	0	4	0
Sisymbrium altissimum	0.4	0.1	16	4
**Salsola kali*	0.1	0.3	4	12
[P]*Townsendia florifer*	0	0.2	0	8
[P]*Lomatium* spp.	0	10	0	52
[P]*Agropyron spicatum*	0	3	0	16
[P]*Balsamorhiza careyana*	0	0.8	0	12
Polemonium micrantha	0	3	0	44
[P]*Crepis atrabarba*	0	0.6	0	4
Lappula redowskii	0	0.2	0	8
Festuca octoflora	0	0.1	0	4
Total	36	81		

[P] Perennial
* Seedling

cheatgrass is favored on south exposures while sandberg bluegrass is favored on north exposures. *Draba verna* occurred with high frequency on south exposures, while *Polemonium micrantha* and *Lomatium* spp. occurred with high frequency on the north exposure. Also, the average amount of canopy-cover provided by plants on the north-facing slope was twice that of the south-facing slope, i.e., 81 percent vs. 36 percent.

The percent botanical composition provided by eight species at points along a line running from south to north over an earth mound is shown in Figure 2. The data show that *Agropyron spicatum, Lomatium* sp. and *Balsomorhiza careyana* are important contributors on north slopes near the crest, while *Bromus tectorum* is poorly represented at the same location. *Polemonium micrantha* was best represented near the bottom of the north-facing slope while *Draba verna* was best represented on the south-facing slope.

Discussion

Cheatgrass is absent or sparsely represented in pristine steppe vegetation (Daubenmire, 1970). The vegetation occupying knob and kettle topography clearly shows the results

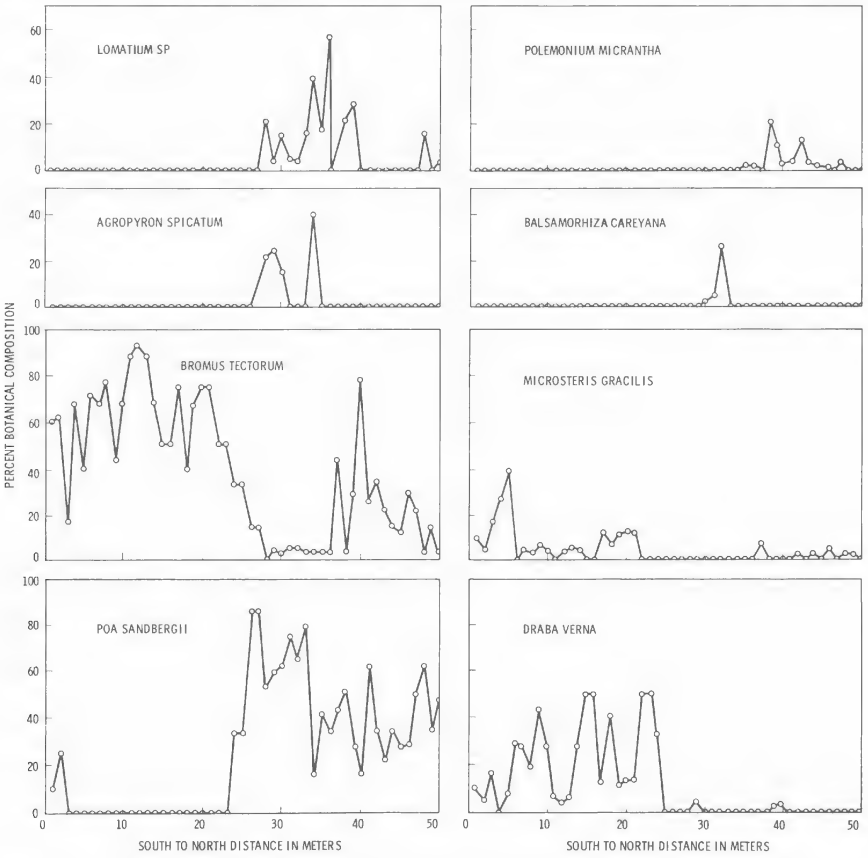


Figure 2. Percent of total botanical composition provided by eight plant species on 50 one-tenth square-meter plots systematically spaced at one-meter intervals along a south-to-north north transect on a cone-shaped knob. The 25-meter mark denotes the knob crest.

of overgrazing by livestock in past years. Even after 30 years without grazing, cheatgrass persists. Bluebunch wheatgrass, *Agropyron spicatum,* is the most important cattle forage plant in the steppe region and is susceptible to damage and even extirpation by prolonged overgrazing. *A. spicatum* is sparse and irregularly distributed on knob and kettle terrain, mostly confined to the steep north-facing slopes of mounds. This suggests that the competition for minerals and soil water by the aggressive alien cheatgrass is an important feature confining the distribution of bluebunch wheatgrass even in the absence of persistent livestock grazing (Harris, 1967). The observations of Dillon (1969) made on the contrasting steep north- and south-facing slopes of a railroad embankment in southeastern Washington showed that bluebunch wheatgrass was able to recolonize the more moist north-facing slope environment but not the dry south-facing slope. A vegetational analysis of knob and kettle topography in Montana (Blinn and Habeck, 1967) showed bluebunch wheatgrass as an important constituent of the vegetation, occurring on all slope exposures but under a precipitational regime averaging 16 inches annually.

Observations by Daubenmire (1970) show that bluebunch wheatgrass is absent in certain pristine stands in the driest portions of the steppe region. In five stands of the *Artemisia tridentata/Poa sandbergii* association, examination of 40 plots yielded only nine herbaceous species in any one stand. Examination of 50 plots on knob and kettle topography (Table 2) yielded only seven herbaceous species in any one stand, and two of these (tumble mustard, *Sisymbrium altissimum,* and Russian thistle, *Salsola kali*) are alien introductions not recorded from Daubenmire's plots.

Field observations using study plots provide the only known basis to objectively recognize subtle changes in plant species composition and abundance with the passage of time and changing land-use patterns.

The differences in species composition and abundance on knob and kettle topography as judged from the expected pristine conditions are due to land-use practices employed prior to the establishment of the Hanford Reservation rather than to construction and operation of nuclear facilities.

Acknowledgements

This investigation was supported by the Washington Public Power Supply System, Richland, Washington.

Literature Cited

Blinn, D. W., and J. R. Habeck. 1967. An analysis of morainal vegetation in the upper Blackfoot Valley, Montana. Northwest Sci. 41: 126-140.

Cline, J. F., and W. H. Rickard. 1973. Herbage yields in relation to soil water and assimilated nitrogen. J. of Range Mgt. 26: 296-298.

Daubenmire, R. 1970. Steppe vegetation of Washington. Wash. Agric. Exp. Sta. Tech. Bull. 62. 131 p.

———. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33: 43-64.

Dillon, C. C. 1967. Exposure may influence grassland establishmeent. J. Range Mgt. 20: 117-118.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum.* Ecol. Mono. 37: 89-111.

Stone, W. A., D. E. Jenne, and J. M. Thorpe. 1972. A.E.C. Research and development Report. Climatography of the Hanford area. Battelle, Pacific Northwest Laboratories, Richland, Washington. BNWL-1605, UC-53.

Received December 16, 1974.
Accepted for publication March 11, 1975.

J. D. Hedlund

Ecosystems Department, Battelle
Pacific Northwest Laboratories
Richland, Washington

Tagging Mule Deer Fawns in South-Central Washington, 1969-1974[1]

Abstract

Two hundred sixty-two mule deer fawns were tagged along the Hanford Reservation reaches of the Columbia River from 1969 to 1974. Twenty tags were returned through 1974. Four tagged animals, all bucks, were killed more than 20 miles from their place of tagging, and one of them was killed 70 miles away. Without tagging of fawns, dispersals would have been undetected.

Introduction

Mule deer, *Odocoileus hemionus hemionus,* are widely distributed throughout southeastern Washington with major populations located in the Blue Mountains and along the breaks of the Snake River and its tributary streams. Rough, steep topography is usually associated with mule deer habitat. The Hanford Reservation in south-central Washington supports a sizeable mule deer herd that has benefited from protection against human intrusions. This protection is provided by security procedures in force for more than 25 years, rather than by topographic inaccessibility. There are probably many more mule deer present on the Hanford Reservation today than there were before its establishment in 1943. Although extensive deer censuses have not been conducted, the population appears to be relatively stable. The purpose of this study was to tag mule deer fawns and to rely on tag returns by hunters to determine if mule deer were indeed dispersing from the reservation into the surrounding areas.

Study Site

This study was conducted on the islands and shoreline associated with that section of the Columbia River which flows for 48 miles through the U.S. Atomic Energy Commission's Hanford Reservation in south-central Washington. This section of the river is not impounded and lies upstream from the pool formed by McNary Dam and downstream from Priest Rapids Dam (Fig. 1).

Vegetation of the surrounding area is mostly undeveloped rangeland dominated by big sagebrush, *Artemisia tridentata* (Daubenmire, 1970). The islands and the riparian strip support scattered stands of lupine, *Lupinus* spp.; buckwheat, *Eriogonum compositum;* absinthe, *Artemisia absinthium;* and ryegrass, *Elymus cinereus.* Shrub cover is sparse but does include occasional thickets of willows, *Salix* spp.; mulberry, *Morus rubra;* and currant, *Ribes cereum* (Hanson and Eberhardt, 1971).

Since little surface water can be found in the surrounding area, mule deer populations tend to remain relatively close to the river during most of the year.

The section of river flowing through the Hanford Reservation was closed to public

[1] Research conducted for the U.S. Atomic Energy Commission under Contract AT(45-1)-1830.

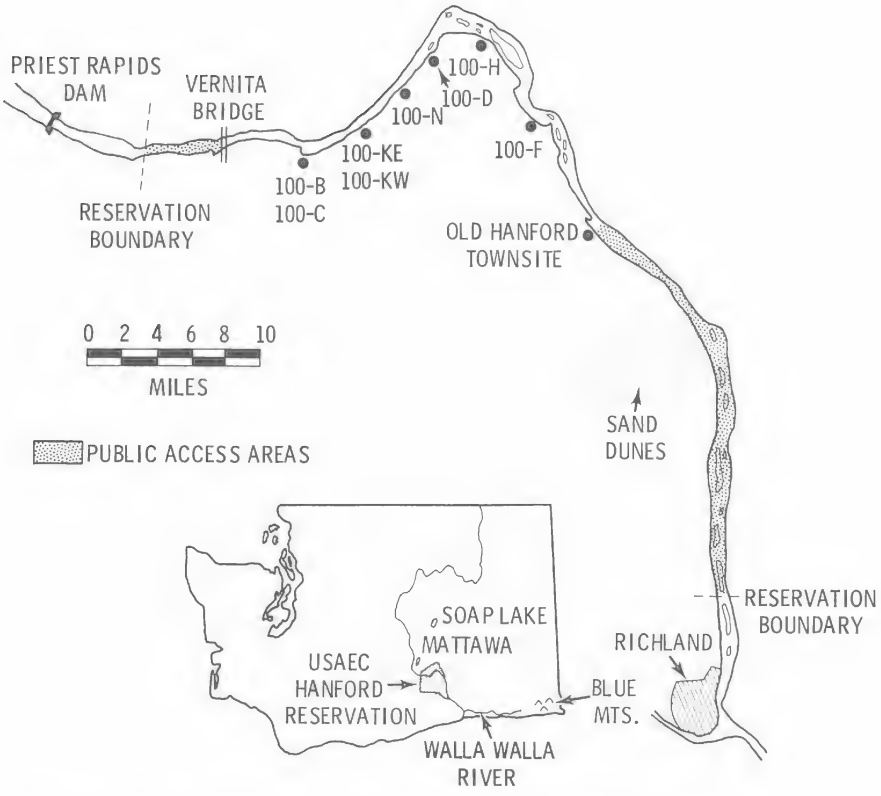


Figure 1. Map of study area and general location within the State of Washington.

use from 1943 to 1971. Since 1971, however, public access has been allowed as far upstream as the old Hanford townsite, 23 miles from Richland, Washington.

Methods Employed in Tagging

A helicopter was used to locate fawns, or does which were suspected of having a fawn nearby. When a fawn was sighted, the tagging crew (usually two people) disembarked and the pilot pursued the fawn alone. If a fawn elected to hide, the helicopter hovered overhead, keeping the fawn's attention, thus allowing the tagging crew to approach close enough for hand-capture. On occasion, some fawns panicked and refused to hide. These were either pursued on foot or driven into the river, where they were taken from the water by personnel in a small boat.

All animals were individually marked with two tags—one furnished by the Washington State Game Department, the other, a large cattle-type tag with 1¼-in. numbers, which can be read at a distance with a spotting scope, for field identification (Fig. 2).

Results

Six consecutive years of tagging results are shown in Table 1. June 1969, the first

Figure 2. A captured fawn which has been fitted with ear tags.

session of intensive tagging, had limited success for the three-day effort, since the tagging crew and the helicopter pilot were inexperienced in the pursuit and capture of fawns. Twenty-four fawns were captured. The next four years—1970, 1971, 1972, and 1973—yielded 51, 52, 53, and 48 fawns, respectively. Only 34 fawns were tagged in 1974 when the entire operation was hampered by hot weather and the dense vegetation brought on by an unusually moist spring.

The response of deer to human intrusion is demonstrated in the tagging results.

TABLE 1. Numbers of mule deer fawns captured and tagged on the Hanford Reservation, 1969-1974.

	1969	1970	1971	1972	1973	1974
Males	13	32	29	31	22	17
Females	11	19	23	22	26	16
TOTAL	24	51	52	53	48	34[1]

[1] One fawn was released before sex was determined.

As restrictions for use of the Columbia River are lifted, fewer fawns are being captured on islands accessible to the boating public, and more are being taken from the restricted-access shoreline areas.

Tag Returns

Tag return information was received mostly through cooperation with the Washington State Game Department. Hunter check stations were the major source of tag returns. Twenty tags from the total of 262 were returned through the fall of 1974; 16 were from hunters, 3 from road-killed animals, and 1 from a dead animal found in an irrigation ditch.

Twelve of 16 tags returned by hunters were from kills near the Columbia River opposite the Hanford Reservation during the annual fall hunting season. An arbitrary ten-mi radius from the tagging point was chosen to distinguish local movements from dispersals.

Four tag returns were from bucks considered out of their home range. One was killed near Mattawa, 25 miles upstream, and another near the confluence of the Columbia and Walla Walla rivers, 50 miles downstream. Movement along the river is to be expected, because of the accessibility of water and vegetative cover. The remaining two returns, however, were from animals which had moved away from the river. One was killed in a farming area 20 miles west of the animal's tagging location, and another made the longest movement to date, a distance of about 70 miles, and was killed north of Soap Lake. Three of the four were killed as yearlings and the other at 2½ years of age. Robinette (1966) indicated that many mule deer bucks do not leave the company of their mothers until their second summer.

Since the Hanford mule deer do not make gross population shifts seasonally, the distances traveled by deer dispersing to the surrounding areas are far greater than expected and would have gone completely undetected if the deer had not been marked as fawns.

Radioactivity in Hanford Deer

Mule deer traveling out of the Hanford Reservation have a certain potential to serve as a pathway for movement of radioactive material from waste management areas to man. The levels of Cesium-137 observed in deer meat from animals killed on the Hanford Reservation during the past few years averaged 0.1 pCi/g wet weight (Bramson *et al.*, 1973). Similar values are reported by Whicker (1973) for deer collected in the mountains of Colorado, far removed from atomic energy facilities. This suggests that the Cesium-137 observed in Hanford deer flesh is primarily from worldwide fallout rather than from a contaminant source on the reservation itself.

Acknowledgements

I wish to thank the many people who assisted with field work, especially R. A. Gies, D. T. McCullugh, T. P. O'Farrell, and the helicopter pilot, B. G. Goins. Much of the tag return data were furnished by the Washington State Game Department. This paper is based on work performed under United States Atomic Energy Commission Contract AT(45-1)-1830.

Literature Cited

Bramson, P. E., J. P. Corley, and W. L. Nees. 1973. Environmental Status of the Hanford Reservation for CY 1972. BNWL-B-278, Battelle-Northwest, Richland, WA.

Daubenmire, R. 1970. Steppe Vegetation of Washington. Wash. Agric. Expt. Sta. Tech. Bull. 62, Wash. State Univ., Pullman.

Hanson, W. C., and L. L. Eberhardt. 1971. A Columbia River Canada goose population, 1950-1970. Wildl. Monogr. No. 28: 1-55.

Robinette, W. L. 1966. Mule deer home range and dispersal in Utah. J. Wildl. Mgmt. 30: 335-349.

Whicker, F. W. 1973. Fallout ^{137}Cs and ^{131}I in Mule Deer and Vegetation, Winter 1972-1973. Contract AT(11-1)-1156, 11th Annual Progress Report to the U.S. Atomic Energy Commission, Department of Radiology and Radiation Biology, Colorado State University, Fort Collins. 4 pp.

Received February 28, 1975.
Accepted for publication April 17, 1975.

Chris Maser

Puget Sound Museum of Natural History
University of Puget Sound
Tacoma, Washington

Characters Useful in Identifying Certain Western Oregon Mammals

Abstract

We are always in need of additional characters that make the identification of mammals more certain. The purpose of this note is to present two such characters.

Marsh Shrews (Sorex bendirii)

Marsh shrews can be distinguished from other western Oregon shrews by their large size, uniform dark coloration, and weakly developed swimming fringes, but they also have small, fleshy projections along the outer edge of each nostril (Fig. 1). The projections are easily seen on either fresh or fluid-preserved specimens, but as a result of drying they are less easily seen on study skins. When students are learning to identify shrews, a difficult group, their attention is often directed to the weakly developed swimming fringes on the feet of the marsh shrew, but these fringes are readily discernible only in young animals. They wear off as an individual ages and are not replaced. The nasal projections, on the other hand, remain evident throughout the life of the animal; they are a singularly distinctive character allowing positive identification. These projections have not been observed on any other species of shrew in western Oregon.

Western Chipmunks (Eutamias)

Western chipmunks are not difficult to identify when a person has in hand a skin and

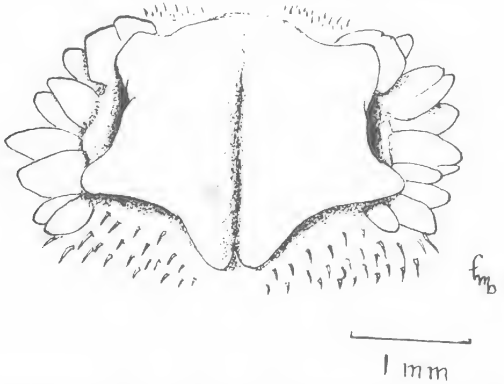


Figure 1. Fleshy projections along each outer edge of the nostrils of an adult, male marsh shrew (*Sorex bendirii*) trapped on 29 March 1969, 2 mi. South of Hebo, Tillamook County, Oregon. The shrew, a fluid-preserved specimen, is in the Puget Sound Museum of Natural History, catalog number 15496.

skull. They are difficult to identify, however, in the cast pellets of owls or the scats of carnivores, because the chipmunks' molars are similar in appearance to those of the smaller western squirrels. Fortunately, the incisors of *Eutamias* differ from those of all other western Oregon sciurids. In *Eutamias* the outer pigmented surfaces of both the upper and lower incisors have fine, but definite, longitudinal striations running the full length of the teeth; such striations have not been observed on the incisors of any other western Oregon squirrels. Although both the Townsend chipmunk (*Eutamias townsendi*) and the yellow pine chipmunk (*Eutamias amoenus*) have these striations, where those species of chipmunk occur together they can easily be determined to genus, and where they occur singly they can readily be identified to species, whether eaten by owls or carnivores.

Acknowledgements

I am indebted to Frank M. Beer, Corvallis, Oregon, who made the illustration in December 1974 and to Richard J. Pedersen, Oregon Wildlife Commission, La Grande, Oregon, for critically reading the manuscript.

Received March 12, 1975.
Accepted for publication April 17, 1975.

Bruce A. Evans
Route 8, Box 478-D
Olympia, Washington

Sensitizing Sherman Small-Mammal Live Traps To Improve Their Efficiency[1]

Abstract

Relative efficiencies of two models of Sherman live traps differed markedly when they were sensitized by trigger adjustment. Equating trap tripping force to body weights of mammals being captured reduced variation in total small-mammal catches between models.

There is considerable disagreement in reported efficiencies between two models of Sherman live traps (Quast and Howard, 1953; Kisiel, 1971) and efficiencies of Sherman and other traps (Wiener and Smith, 1972). Perhaps these conflicts reflect sensitivity differences among traps. Only Wiener and Smith (1972: 872) report sensitivity affecting relative efficiencies of traps. They reported their Museum Special snap traps were more sensitive—based on traps tripped without catches—and more efficient than Sherman live traps and others tested.

This paper describes a study I did to improve sensitivity and efficiencies of Sherman live traps reported faulty by Lindsey, Anthony, and Evans (1974: 276). The traps were standard 1967 and 1970 models of Sherman, advertised as "non-folding; 3 x 3 x 10 inches; galvanized iron (3310G); live animal traps" (product brochures, 1967 and 1970, H. B. Sherman, DeLand, Florida). During another study, the 1967 model repeatedly outperformed the 1970 model in catching deer mice (*Peromyscus maniculatus*) and other small forest-mammals. I believed the difference I observed could lead to erroneous study conclusions. Therefore, I decided to study relative efficiencies of the two models and correct any obvious deficiencies causing significant difference in total small-mammal catches between models.

Ten 1967 and ten 1970 model traps were randomly selected from about 100 of each model being used by the U.S. Fish and Wildlife Service (USFWS) in seed protection studies. A 4-ha stand of 40- to 50-year-old Douglas-fir (*Pseudotsuga menziesii*) 5 km south of Olympia, Washington served as the study area. Traps were placed at ten, randomly located, fixed trapping stations, the closest being 40 m apart. One 1967 and one 1970 model trap were placed side by side at each station. Each pair of traps was permanently assigned to a station, and in each pair the traps were exchanged each active day to reduce position bias. Traps were set for two consecutive days and left unset for five days. Traps were scraped clean and new bedding provided before each active period and after a catch was made. Each active day, traps were baited with fresh peanut butter and rolled oats. All trapped animals were removed from the study area to eliminate trap-proneness bias. Trapping was done from December 11, 1971 through January 30, 1972 in two equal test periods.

[1] Reprints may be obtained from U.S. Fish and Wildlife Service, Route 4, Box 500, Olympia, WA 98502.

In the first test, all traps were sensitized by a widely used method, that of trigger adjustment. This was done by adjusting the trigger-door catch until a light tap on the back of the trap sprung the trap. Sensitivity was checked each day by tapping the trap and further adjustment was not necessary during this test period. Results (Table 1) showed that the 1967 model was significantly more efficient than the 1970 model for total captures ($X^2=48.29$, df=1, $P<.01$).

TABLE 1. Results of a removal trapping study comparing relative efficiencies of 1967 and 1970 models of Sherman live traps by trigger adjustment sensitizing (Test I), and by standardizing the trap tripping force (Test II). Catch is expressed as individuals captured per 100 trap nights.

	Test I		Test II	
Species	1967 model	1970 model	1967 model	1970 model
Peromyscus maniculatus	24	1	20	17
Clethrionomys occidentalis	25	1	3	4
Sorex trowbridgii	5	0	8	14
Total all species	54	2	31	35
Expected trap nights	80	80	80	80
Traps tripped w/o catch	4	0	7	10
Observed trap nights	76	80	73	70

Traps tripped without a catch (Table 1) indicated that the 1967 model traps were more sensitive than the 1970 model traps. Examination of traps revealed a difference in tension springs and trigger-door catches between models. Treadle- and door-springs in 1970 model traps had 15 or 16 coils. Nine 1967 model traps had springs with 5 coils, the other trap had springs with 10 coils. The 1970 model traps also had a more secure trigger-door catch—a rolled metal edge compared to a smooth, slightly hooked edge in 1967 model traps. The combined effect of greater tension in both treadle and door springs and the more secure catch in 1970 model traps necessitated a greater weight on the treadle to trip traps—30.3 gm (range 21-35 gm) for 1970 model traps compared to 11.3 gm (range 2-55 gm) for 1967 model traps. Readjusting triggers did not significantly reduce this tripping force. Evidently body weight of the captured species affected trap efficiencies—deer mice averaged 17.1 gm (range 11.5-26.4 gm); red-backed voles (*Clethrionomys occidentalis*) averaged 18.0 gm (range 13.4-20.0 gm); Trowbridge shrews (*Sorex trowbridgii*) averaged 4.7 gm (range 4.3-5.8 gm).

For the second test, all traps that would not trip with a 15-gm weight on the distal end of the treadle were resensitized by bending the arm of the treadle-spring away from the treadle until 15 gm tripped the trap. The one 1967 model with the ten-coil treadle-spring and all 1970 model traps were resensitized by this method. After adjustment, the 1970 model traps tripped with 10.7 gm (range 3-15 gm) on the treadle and the 1967 traps with 7.3 gm (range 2-15 gm) on the treadle. Sensitivity was checked each active day with a 15-gm weight; readjustments were not necessary and pre- and post-test tripping force did not vary. In this test (Table 1) the difference in total catches between models was not significant ($X^2=0.24$, df=1, $P>.05$).

I believe these tests demonstrated the effect of sensitizing on efficiency of Sherman traps. Trigger adjustment did not adequately sensitize 1970 models and some 1967

models. Adjusting trap tripping force to body weight of mammals improved trap response, and uniform sensitivity resulted in more equable efficiencies of the two models.

After this demonstration, tripping force in all remaining USFWS traps needing resensitizing was reduced by affixing lead to the end of the treadle.. The lead facilitated readjustment to specific study needs (for example, 2-4 gm for total species sampling; 11 gm for winter deer-mouse tagging studies) more than bending springs. Lindsey (personal communication) wrote: "Both our galvanized and aluminum (Sherman 3310A, 1970 design) models required resensitizing. The aluminum model required 45 to 75 grams to trip the treadle after using the trigger adjustment method and before lead was added to resensitize the traps. After resensitizing, the reliability and capture success for all trap models and designs was similar in later field studies."

Various trigger release mechanisms have been devised for greater sensitivity and reliability of live traps (Fitch, 1950; Howard, 1953). Highly sensitive Sherman and Sherman-type traps can be specially ordered. I believe that the trigger mechanism in standard design Sherman traps is reliable and, as pointed out, can be highly sensitized by reducing trap tripping force.

There is general agreement that several types of traps should be used to improve accuracy of sampling small-mammal populations (Wiener and Smith, 1972; Nellis, Terry, and Taber, 1974). Where live trapping is required, however, other investigators may find it desirable to check and sensitize their traps as described herein to improve their reliability.

Acknowledgements

J. Evans, Project Leader of the Forest-Animal Damage Control Research Project (U.S. Fish and Wildlife Service, Olympia, WA 98502) guided the study and aided in the preparation of the manuscript.

Literature Cited

Fitch, H. S. 1950. A new style live-trap for small mammals. J. Mammal. 31(3): 364-365.
Howard, W. E. 1953. A trigger mechanism for small-mammal live traps. J. Mammal. 34(4): 513-514.
Kisiel, D. S. 1971. Effect of two sizes of Sherman traps on success of trapping Peromyscus and Reithrodontomys. Amer. Midland Nat. 87(2): 551-552.
Lindsey, G. D., R. M. Anthony, and J. Evans. 1974. Mestranol as a repellent to protect Douglas-fir seed from deer mice. Proc. 6th Vert. Pest Conf., Anaheim, CA., p. 272-279.
Nellis, C. H., C. J. Terry, and R. D. Taber. 1974. A conical pitfall trap for small mammals. Northwest Sci. 48(2): 102-104.
Quast, J. C., and W. E. Howard. 1953. Comparison of catch of two sizes of small-mammal live traps. J. Mammal. 34(4): 514-515.
Wiener, J. G., and M. H. Smith. 1972. Relative efficiencies of four small-mammal traps. J. Mammal. 53(4): 868-873.

Received April 14, 1975.
Accepted for publication May 8, 1975.

E. F. Hooven
Forest Management Department
and
R. F. Hoyer[1]
R. M. Storm
Zoology Department
Oregon State University
Corvallis, Oregon

Notes on the Vagrant Shrew, Sorex vagrans, in the Willamette Valley of Western Oregon[2]

Abstract

Sorex vagrans is one of the commonest small mammals in the riparian zones of the Willamette Valley in western Oregon. Its habitat requirements are best met in heavily grassed, meadow-like situations, where it is associated often with *Microtus canicaudus* and *M. townsendii*. Sexual maturation for the male vagrant shrew occurs in late January and pregnant females were recorded in February. Two main reproductive periods occur in spring and fall. Postpartum pregnancies were noted for adult females, and 20 percent of the young of the year become sexually mature and reproductive by midsummer. Mean size of litter is six. The young weigh about 0.35 gm at birth, reach a top weight of 4 to 5 gm at 19 days, open their eyes at 21 days, are weaned at 24 to 25 days, and probably disperse at 4 to 5 weeks of age.

Adult males are heavier than adult females; immature individuals are lighter, but only slightly smaller, than adults. The vagrant shrew eats about 8 gm of food per day: normally small invertebrates such as insects, larvae, and earthworms, plus some plant material. Principal known predators are the rubber boa, owls, and possibly garter snakes.

Introduction

The vagrant shrew (*Sorex vagrans*) is found throughout Oregon (Hall and Kelson, 1959). It has been considered an intergrading chain of subspecies along the Pacific Coast from southern British Columbia through western Oregon and into California (Findley, 1955). Only observations on the subspecies *S. v. vagrans* in the Willamette Valley are made in this paper.

The purpose here is to add to general knowledge concerning *Sorex vagrans* from data gathered during 1973 about general habitat preference, associated small mammals, yearly age classes, reproduction and development of young, monthly weights and total lengths, and food and predators.

Shrews collected by live-trapping and by live-capture from beneath old boards, tins, and pieces of plywood numbered 369 individuals. Live-captured animals were killed, except for some females having litters or suspected of being pregnant, and were measured and examined post-mortem. Shrews found dead in live-traps were treated similarly. Shrews that could not be examined immediately were frozen in plastic sacks and stored for periods of less than one week.

Observations on female shrews and their litters were made in small aquariums. All were supplied liberally with food, water, and nesting material.

[1] Present address, 2730 N.W. Arnold Way, Corvallis, Oregon 97330.
[2] Paper 940, Forest Research Laboratory, School of Forestry, Oregon State University, Corvallis, Oregon 97331.

Study Area

The Willamette Valley lies between the Cascade Range and the Coast Range and extends from Portland (lat. 45°30″ N) southward for about 200 kilometers to a point near Cottage Grove (lat. 43°40″ N), where the two ranges converge. The Willamette River drains northward into the Columbia River and is fed by many tributaries from both the Cascade and Coast ranges. Elevation decreases from 200 meters at Cottage Grove to 61 meters at Portland. Recent alluvium is widespread along the streams. Topography is a broad, moderately flat valley floor with groups of low hills.

The climate is humid, with temperatures modified by air masses pushing prevailingly northeastward from the Pacific Ocean. Summers are dry and occasional periods of low humidity are accompanied by easterly or northerly winds. Precipitation occurs mostly in fall and winter. Total precipitation during 1973 was 98.35 cm (38.72 in.) at Corvallis, although the 30-year average was 101.6 cm (40 in.). During 1973, from April 23 to September 18 (148 days), only 7.48 cm (2.95 in.) of rain fell. In late spring the surface of the clay-loam soil becomes dry, hard, and cracked. Mild temperatures occur throughout the year. Coldest weather occurs during December and January, with little soil freezing. Warmest weather occurs in July and August.

Habitat and Associates

No attempt was made to determine habitat requirements of the vagrant shrew. Specimens have been taken by other workers in meadows, dry uplands, moist woods and marshes (Jackson, 1928; Bailey, 1918, 1936; Dalquest, 1948; Jameson, 1955; Clothier, 1955). We found the vagrant shrew accounted for only 9 percent of all small mammals caught on both timbered and cutover conifer forest lands above the riparian zones. *S. trowbridgii* accounted for 25 percent. In meadowlands, where grasses such as velvet grass (*Holcus lanatus*), oatgrass (*Danthonia californica*), hairgrass (*Aira caryophyllea*), and dogtail (*Cynosurus echinatus*) became dense and formed the predominant cover, vagrant shrew density increased to 30 percent and the Trowbridge shrew decreased to 3 percent of the small mammal population. *S. trowbridgii* appeared to prefer a vegetative cover dominated by brush and forb species, with lesser amounts of grass. Presence of either shrew did not appear to be related to proximity of water. The vagrant shrew was most numerous at lower elevations with a mean annual precipitation of 100 cm, but decreased in numbers as elevation and precipitation in the Coast and Cascade ranges increased. This suggests that *S. vagrans* prefers a drier, grassier habitat than does *S. trowbridgii*.

The main mammalian associates of the vagrant shrew were the gray-tailed vole (*Microtus canicaudus*), Townsend's vole (*M. townsendii*), deer mouse (*Peromyscus maniculatus rubidus*), jumping mouse (*Zapus trinotatus*), Trowbridge's shrew, Oregon creeping vole (*M. oregoni*), and the shrew-mole (*Neurotrichus gibbsii*). In meadows of major river valleys, the most common associates were the gray-tailed and Townsend's vole, Camas pocket gopher (*Thomomys bulbivorus*), and the Townsend's mole (*Scapanus townsendii*). Above the valley floor where meadowland joined forest, the habitat was shared by all of the small mammals, but definite preferences were observed. The vagrant shrew, gray-tailed vole, and Townsend's vole were caught in grassy meadows, but Trowbridge's shrew and the creeping vole were caught on the edge or in the forest. The deer mouse occurred in all habitats, but preferred nongrassy areas. At higher elevations (up to 240 m) with south- and east-facing slopes and dense grass cover,

the small mammal population was composed primarily of 4-10 percent Trowbridge's shrew, 40-50 percent creeping voles, 30-35 percent vagrant shrews, 5-17 percent deer mice and Townsend's chipmunks (*Eutamias townsendii*), and 3-6 percent jumping mice. The gray-tailed vole and Townsend's vole were confined to riparian meadowlands and did not occur at higher elevations.

Age Classes

The vagrant shrews caught were classified as juvenile, subadult, or adult. Separation was based on pelage, weight, total length, and development of the reproductive systems. No attempt was made to estimate age of shrews on the basis of tooth wear, as was done by Clothier (1955). Instead, major emphasis was placed upon bimodal development of the testes size for males and the width of the uterine horn, measured near the base, for females.

Juvenile shrews were considered nestlings until time of dispersal from the nest. After dispersal, young of the current year that had not reached sexual maturity were classified as subadults. No difficulty was encountered in separating juveniles and subadults from older animals. Subadults, which first appeared in late March, were smaller, lighter in weight (usually less than 5 gm), and possessed immaculate light brown pelage. Their densely furred tails were unscarred and distinctly bicolored. Internal examination showed that the subadult males possessed testes less than 2 mm in length, with no evidence of sperm, and the females had uterine horns less than 1.0 mm wide, measured near the base.

The distinction between subadults and adults was determined by the developmental status of internal reproductive organs in relation to known periods of reproductive activity. Pelage condition and color and, to a lesser extent, size and weight were correlated with the established reproductive status. In establishing these criteria, sexually mature adults of the previous year were compared with shrews of known ages reared in confinement. Use of these criteria was facilitated by field observations, where a natural contrast between subadult and adult shrews exists, especially in the spring.

Little perceptible reproductive activity was noted during the late fall months, but most adult male shrews caught after December had enlarged testes and manifested prominent and strongly odiferous flank glands. The females had conspicuous, turgid-appearing reproductive tracts.

In late February and early March, captured shrews were approaching sexual maturity. Males had testes longer than 3 mm and possessed sperm. Females had uterine horns wider than 1.0 mm and were pregnant, or lactating. In conjunction with the advanced internal status, both sexes were generally large and heavy (more than 5 gm), and many had progressed into the molt, changing from dark to light pelage, but did not display the characteristic immaculate light brown pelage exhibited by recently weaned shrews. Usually, tails of the adults were not distinctly bicolored, were less densely furred (some nearly naked), and had a scaly appearance with invariably some degree of scarring. Usually, none of these adult characteristics was disguised by the molt. The pelage progressively deteriorated with time, so that from April through June there was no difficulty in distinguishing adults from the subadult shrews produced during this reproductive period.

From mid-June through early September, brood nests and litters, common during the spring breeding season, were no longer found at ground level, presumably because

of increased temperatures and lower humidity. However, productively active shrews were found. After the spring reproductive season, distinguishing sexual maturity by external appearance alone was progressively more difficult. By the end of the summer, there existed gradation in pelage types between shrews thought to have been weaned recently and current-year adults born early in the spring. But, also, some overlapping in external appearance existed between spring-produced shrews and surviving adults from the previous year, so our primary means of distinguishing adults from subadults from June through October was internal examination of the reproductive tracts.

During spring and early summer, populations of *S. vagrans* were two-thirds subadult (Table 1). The ratio of subadults to adults declined in late summer but sharply

TABLE 1. Monthly catch of *Sorex vagrans*.

	Adults			Subadults				
Month	Male	Female	Both	Male	Female	Both	Percentage of all	All
Jan.	20	6	26	6	19	25	49	51
Feb.	8	5	13	0	2	2	13	15
Mar.	18	11	29	0	0	0	0	29
Apr.	4	16	20	18	26	44	69	64
May	4	5	9	11	8	19	68	28
June	11	7	18	8	16	24	57	42
July	9	3	12	4	10	14	54	26
Aug.	3	1	4	1	0	0	20	5
Sept.	4	5	9	3	1	4	31	13
Oct.	1	4	5	11	13	24	83	29
Nov.	1	2	3	10	9	19	86	22
Dec.	2	2	4	24	17	41	91	45
Totals	85	67	152	96	121	217	—	369

increased in fall, which indicated that the annual turnover in population was near completion by mid-summer or early fall. Life span for the vagrant shrew is, therefore, short, longevity being similar to that observed for *S. trowbridgii* in California (Jameson 1955).

Nests

Three types of nests were observed in the field: resting, brood, and cold-weather. Resting nests were about 6-8 cm in diameter, shallow, cup-shaped, usually without a top, and most often constructed of grass. The cup-shaped interiors were 2 cm in diameter —just large enough for the occupancy of one shrew. Brood nests were well built, round or oval, and usually measured from 9 to 14 cm in diameter and 5 to 7 cm in height. Construction consisted of a loose outer layer and a more compact inner layer. Inner nesting chambers were from 2 to 3 cm in diameter, with one or two exits. The most common nest materials were grass, moss, and leaves; but paper, plastic, feathers, and other materials also were used. Cold-weather nests were from one-half to two-thirds the size of brood nests. They were round or oval, well constructed, with one or two entrances to the inner chamber. Vagrant shrews were caught often in abandoned nests of voles, deer mice, and moles.

Reproduction

Reproductive information for *S. vagrans* was acquired primarily from data on field observations, rearing litters in captivity, and post-mortem examinations. Testes length was measured by a millimeter ruler through a hand lens. Samples were taken from testes or epididymis and examined microscopically for sperm.

Testes of juvenile males ranged from barely visible to 1.0 mm in length. Testes of subadults ranging from 1.0 to 3.0 mm were sampled, but no sperm were noted. Of the subadults examined in December, when testes length ranged from 3 to 4 mm, more than one-half (13 of 24) were in the process of meiosis. Sexually mature males with testes from 3.0 to 6.0 mm in length were noted in midwinter and through the spring. Adult males were sexually active at least into July, when testes were large (4 to 6 mm) and contained sperm. No male vagrant shrews were found with olive-colored, flaccid testes that indicate regression, as reported for *S. trowbridgii* (Jameson 1955).

Juvenile female shrews had extremely slender uterine horns, and those of non-breeding subadults were less than 0.5 mm wide. In January, widths of uterine horns of adult nulliparous females ranged from 0.5 to 1.0 mm. In February, width of uterine horns ranged from 1.0 to 2.0 mm and pregnant females were recorded. By March, 36 percent of adult females were pregnant or lactating. The number increased to 90 percent in April and May and to 100 percent in June and July. These observations are similar to those reported for *S. v. halicoetes* in California (Rudd 1955). The mean number of embryos was six, with a range from two to eight for 18 females. Litters of nine young, however, had been observed before this paper was begun.

Field observations show a second period of reproductive activity in the fall from September through mid-November. Numerous brood nests, some containing litters, were observed, and there was an increase in the capture of subadult shrews during this period (Table 1). The fall molt, from light to dark pelage, coincided with this reproductive period, and sexual status among the molting shrews continued to be determined by post-mortem examination. During the fall, recently weaned shrews, however, exhibited the characteristic light brown fur of all subadults, which contrasted sharply with the older, darker, molting shrews. These small, brown, nonreproductive shrews comprised the majority of the subadults collected during the fall. Sometime during early or midwinter these subadults also molted, for by late January all shrews possessed dark pelage.

Although the sample is insufficient to warrant thorough analysis, some generalizations are possible in light of our observations and the data presented in Table 1. There are two main reproductive periods for *S. vagrans* in the Willamette Valley—spring and fall. Extent of litter production during the summer is not known, however. Two distinct subadult samples of four months duration each (April-June and October-January) arise from the two known periods of reproductive activity (Table 1). The similarity in size of these samples, 101 and 109, suggests that the spring and fall seasons are of equal importance to the species. But because of observations not depicted by the data, we estimate that the spring-cycle output exceeds the fall production. Of the 44 reproductive females, 80 percent were old adults caught from February to July, and 20 percent were current-year adults caught from the beginning of September to the end of November.

Although the overall sex ratio closely approximated 1:1 (181 males to 188 females), some distortion in the opposite direction occurred within the adult and subadult samples (Table 1). Moreover, the ratio of adults to subadults (152:217) suggests a rapid turnover. During the early part of the fall reproductive period, we found few adults that we considered to be survivors from the previous year. The indication is that a complete turnover occurs in about one year. The percentage decrease in subadults at two intervals during the year (August-September and February-March) is noteworthy because it suggests that shrews produced in spring reach sexual maturity by late summer, and fall-produced shrews reach maturity by late winter. Of 42 shrews caught in June, 9 males and 18 females were thought to be young-of-the-year. Post-mortem examination revealed that three were sexually active and three had nearly mature reproductive organs. In September, of 13 shrews captured, 64 percent of the 11 current adults were in reproductive status.

Observations were made on 17 litters that included 93 young. Fifteen captive females produced 89 newborn with a mean litter size of 5.9 (range, 2-8). Of these, 17 percent died within two days of birth and 49 percent survived for 25 days or longer. Young were born naked, were dark pinkish-red, and weighed about 0.35 gm (Fig. 1). On the seventh day, when one-third grown, they were still hairless and blind, and their weight had increased to about 1.9 gm. Sex could be determined externally at 14 days. At 19 days and before their eyes opened, the shrews reached a weight of 4 to 5 gm; their eyes opened at 21 days, and a slight reduction in weight occurred for several successive days. The lost weight—presumably because of weaning—was regained, however, and at 41 days average weight of the young approached that of adults. Captive litter mates remained in the nest until weaning, which occurred at 25 days. These observations differ from those of Johnston and Rudd (1957) on the salt marsh shrew (*S. v. halicoetes*) in California. They reported that the eyes opened at 14 days, and weaning extended from day 16 to day 20.

Even after weaning, captive litter mates were reluctant to leave the nest. In the field, too, litters of young that appeared to be fully weaned were captured in the brood nest. Johnston and Rudd (1957) reported that *S. v. halicoetes* young remained in the nest to about the fifth week, and Eisenberg (1964) noted that immature *S. vagrans* will seek each other's company.

Measurements

Measurements (Table 2) were taken of individuals captured alive and killed and of individuals caught in live-traps. Weights of the sacrificed shrews (Fig. 2) were consistent with weights of live, free-roving shrews. Weights of shrews found dead in traps were necessarily less than weights of live-caught animals, 10 percent less for adults and 17 percent less for subadults. Weights of trap-dead animals were not included in data for construction of Figure 2.

During winter, the mean weight of adult females was about 5 gm. Weight increased to over 6 gm for lactating and pregnant females (discounting weight of embryos) during spring and early summer. An adult captive female with a 21-day-old litter weighed 5.9 gm. Seven other females had a mean weight of 6.7 gm when the young were 25 days old. As demands of nursing slackened, weights of adult females decreased slightly.

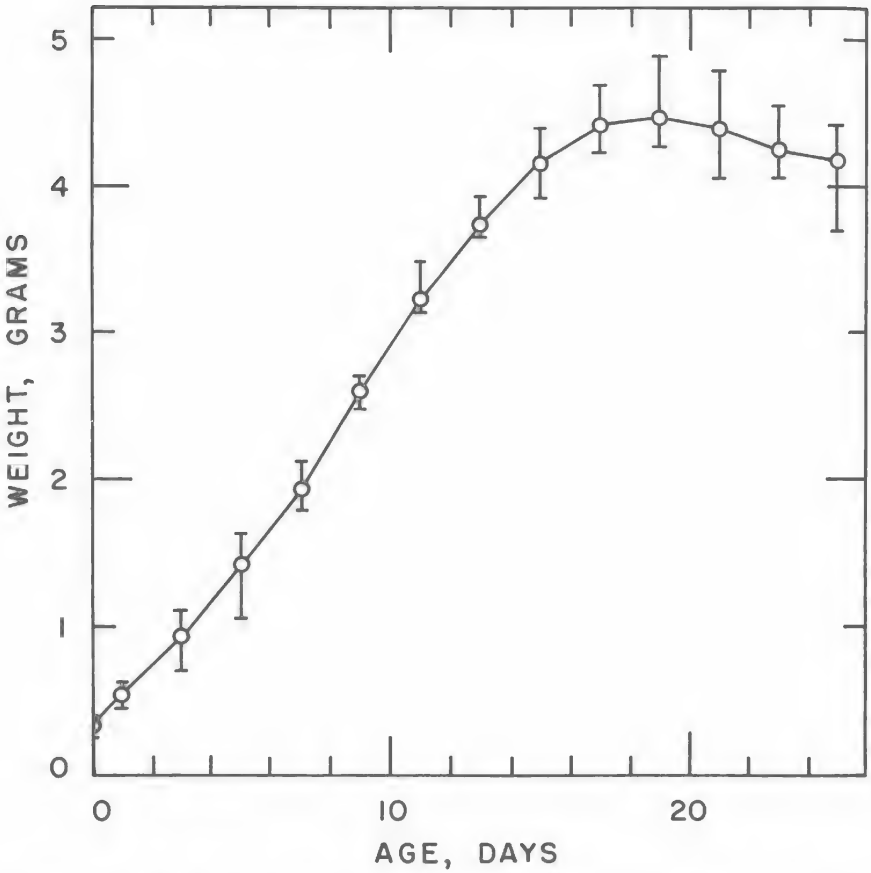


Figure 1. Average change in weight of individuals in six litters of *Sorex vagrans*. Each point from day 1 represents the average weight of 30 young from the six litters. The birth weight at day 0 is extrapolated from eight litters that contained 40 newborn. Bars on the vertical lines represent extremes in weight of the litters.

Mean weight of adult males was over one gm more than weight of quiescent females during winter, and they remained heavier than females as the seasons progressed.

Captive juveniles were heaviest between 19 and 21 days (Fig. 1), after which their weights decreased. The decrease was temporary, however, because one retained litter of captive subadults reached adult weight at about six weeks. From field observations, we estimate that developing subadults in the field approached adult weight more gradually.

A synchronous change in mean live weights occurred for both sexes and ages throughout the seasons, with the lightest weights occurring in summer, the driest and warmest season of the year in the Willamette Valley. Only 12 percent of the total number of shrews was caught during that period. Low humidity and warm nights without formation of dew could cause water deprivation and potentially affect survival and weight of shrews through dessication.

TABLE 2. Measurements for vagrant shrews, in grams and millimeters (mean, standard error of the mean, and range).

Sex	Age	Number	Range	Mean	S.E.
			WEIGHT		
Male	Adult	42	4.87-7.80	6.3	0.13
Female	Adult	48	4.19-7.75	5.5	.10
Male	Subadult	73	3.50-6.11	4.6	.06
Female	Subadult	64	3.39-5.74	4.4	.06
			TOTAL LENGTH		
Male	Adult	62	88-109	100.9	.52
Female	Adult	65	88-113	101.9	.58
Male	Subadult	9	83-107	97.5	.39
Female	Subadult	117	87-106	96.4	.42
			LENGTH OF TAIL		
Male	Adult	84	33-43	38.1	.24
Female	Adult	65	32-46	38.3	.29
Male	Subadult	97	30-43	37.9	.22
Female	Subadult	116	31-44	37.5	.21
			LENGTH OF HEAD		
Male	Adult	84	18-23	20.6	.10
Female	Adult	65	19-23	20.9	.11
Male	Subadult	96	18-22	20.8	.07
Female	Subadult	117	19-22	20.4	.07

Differences in total lengths varied slightly (Fig. 3), with no significant differences because of sex. The mean length of subadults for an entire year, however, was slightly shorter than that for adults. Two subadults, born in captivity, at 42 days had a total length of 95 mm, tail length of 36 mm, and head length of 20 mm. Two other subadults, caught wild in the nest and appearing to have been just weaned, measured 103 mm total length, 39 mm tail length, and 21 mm head length. Dispersing young are only slightly shorter than adults and have approached their maximum skull size. This observation agrees with that of Clothier (1955) in Montana. Table 2 gives a comparison of yearly mean measurements of 362 vagrant shrews.

Food Habits

Food for *S. vagrans* has been noted generally as being insects, larvae (Bailey, 1936), other small invertebrates, earthworms and some plant material (Clothier, 1955). Both the vagrant shrew and *S. trowbridgii* have been credited with considerable depredation on Douglas-fir (*Pseudotsuga menziesii*) seed on logged-over forest lands (Moore, 1940).

Captive vagrant shrews were kept alive easily for several months or more by feeding them the carcasses of small rodents such as *Peromyscus* sp. and *Microtus* sp. and one- to two-day-old chicks and quail (*Coturnix* sp.). Earthworms (Annelida), centipedes (Chilopoda), grasshoppers and crickets (Insecta), and small slugs (Gastropoda) were accepted as supplemental food. Dampwood termites (*Zootermopsis angusticolis*) were eaten eagerly. Commercial canned baby food (beef, veal, or chicken—all without vegetables) was accepted readily.

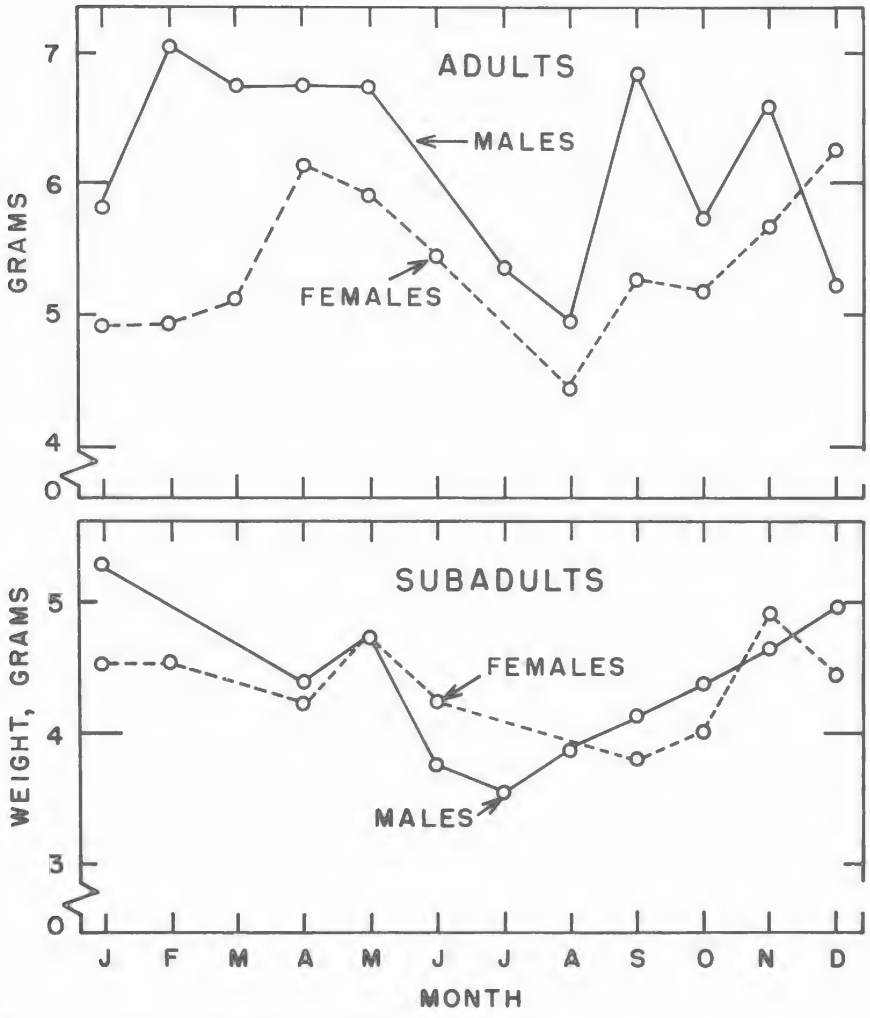


Figure 2. Monthly mean weights of live *Sorex vagrans*.

Records on 30 days of feeding show that each of four vagrant shrews, confined in a glass-fronted box 30 by 30 by 30 cm, ate 8.69 gm of baby food per day, plus some earthworms. A female, nursing six young, was estimated to eat 25 gm per day from rodent carcasses during the late stages of litter development.

The vagrant shrews also ate Douglas-fir seed, as noted by Moore (1940). They ate about 15 percent of the Douglas-fir seed that had been added to the bait of live-traps during small-mammal studies. Death occurred, however, regardless of the amount of seed available, and conifer seeds were not accepted as food during captivity.

Behavior

Field observations indicate that *S. vagrans* is solitary by habit. Except for a family

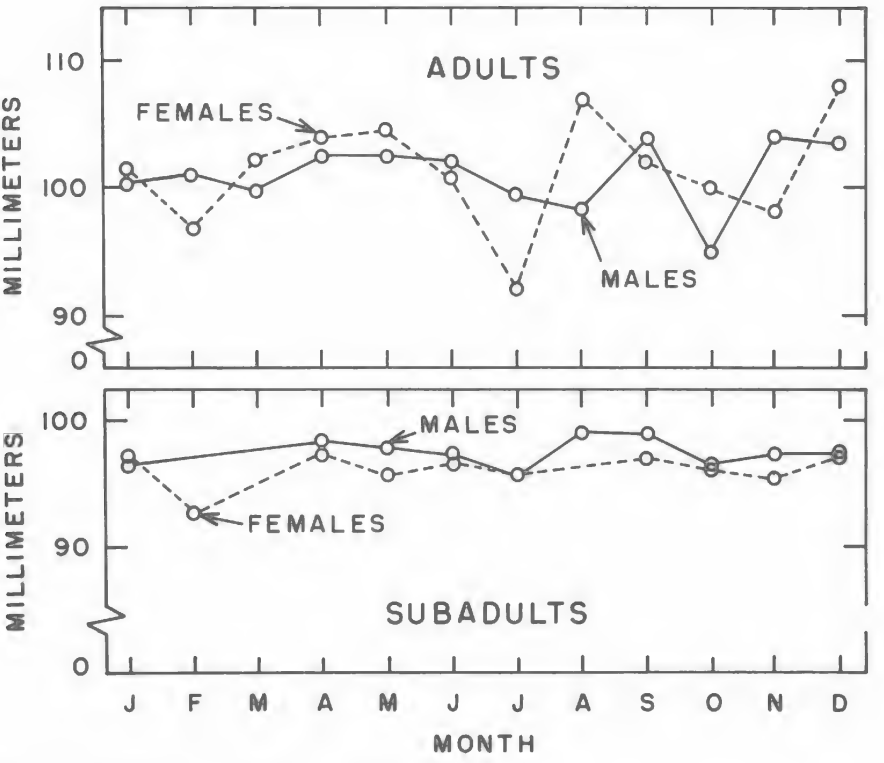


Figure 3. Monthly mean total lengths of *Sorex vagrans*.

group of a mother and young, two or more shrews rarely were found together. When multiple catches occurred, the combination was always an adult and a juvenile, or undispersed nestlings. Resting nests are further evidence of this solitary habit, as the nest cavities are large enough for only one individual.

Captured shrews were restless when confined closely, but were infrequently antagonistic toward each other. They nested together when forced by restrictive conditions, but adults preferred separate areas of about 25 square cm with cover for resting and sleeping quarters.

Observations on confined shrews suggest that subadults are dominant over adults and adult females are dominant over adult males. Adult females, however, defended their litters, and trespassing shrews were driven from the brood nest. Litters also were defended vigorously against small rubber boas (*Charina bottae*).

Predators

The red-spotted gartersnake (*Thamnophis sirtalis*) and the Northwestern gartersnake (*T. ordinoides*) ate vagrant shrews in captivity, and the shrew is a food item of the rubber boa in western Oregon. The rubber boa has a preference for nestling and juvenile shrews and was found commonly under material sheltering aboveground nests of the vagrant shrew.

Captive weasels (*Mustela frenata* and *M. erminea*) refused to eat shrews. The shrews offered, however, were adults with well-developed musk glands. Nestling and subadult shrews without glands conceivably could be preyed upon by weasels.

Owls also prey upon shrews. Shrew species were found to be 2.91 percent, 1.81-10.7 percent, and 10.15 percent of the diets of long-eared owls, barn owls, and great horned owls (Maser and Brodie, 1966) in the Willamette Valley. In California, items in pellets of short-eared owls were about 3.5 percent shrews (Johnston and Rudd, 1957).

Literature Cited

Bailey, V. 1918. Wild animals of Glacier National Park: the mammals. U.S. Govt. Printing Office. 102 pp.

———. 1936. Mammals and life zones of Oregon. North Amer. Fauna No. 55. U.S. Dept. of Agric. 416 pp.

Clothier, R. R. 1955. Contribution to the life history of *Sorex vagrans* in Montana. J. Mammal. 36: 214-221.

Dalquest, W. W. 1948. Mammals of Washington. Univ. Kansas Publ., Mus. Nat. Hist. 2: 1-444.

Eisenberg, J. F. 1964. Studies on the behavior of *Sorex vagrans*. Am. Midl. Nat. 72: 417-425.

Findley, J. S. 1955. Speciation of the wandering shrew. Univ. Kansas Publ., Mus. Nat. Hist. 9: 1-68.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. Ronald Press Co., New York. 2 vols.

Jackson, H. H. T. 1928. A Taxonomic review of the American long-tailed shrews. North Am. Fauna 51: 1-238.

Jameson, E. W., Jr. 1955. Observations on the biology of *Sorex trowbridgii* in the Sierra Nevada, California. J. Mammal. 36: 339-345.

Johnston, R. F., and R. L. Rudd. 1957. Breeding of the salt marsh shrew. J. Mamm. 38: 157-163.

Maser, C., and E. D. Brodie, Jr. 1966. A study of owl pellets contents from Linn, Benton, and Polk counties, Oregon. Murrelet 47: 9-14.

Moore, A. W. 1940. Wildlife animal damage to seed and seedlings on cutover Douglas-fir lands of Oregon and Washington. Tech. Bull., U.S. Dept. Agric. 706.

Rudd, R. L. 1955. Age, sex, and weight comparisons in three species of shrews. J. Mammal. 36: 323-339.

Received August 19, 1974.
Accepted for publication May 8, 1975.

William N. Orr
and
John Faulhaber

A Middle Tertiary Cetacean from Oregon

Abstract

Fossil vertebrae of a primitive cetacean are reported from a marine siltstone and sandstone unit in the Northwestern Oregon Cascades known informally as the "Butte Creek Beds."

This unit has variously been dated as late Oligocene to early Miocene on the basis of marine invertebrates and leaf florules. The fossil record of middle-Tertiary cetaceans is noted with attention to their trophic position and remarkably low diversity.

Introduction

Marine vertebrate fossils are rare because of the remarkable efficiency of marine scavengers and the abrasive capacity of the high-energy strand environment. Although numerous fossil marine invertebrates have been reported in Oregon (Condon, 1906; Marsh, 1915; Packard and Kellogg, 1934; Emlong, 1966), Emlong's work represents the only description of pre-Miocene archaic cetaceans in this area. Emlong (1966) has described a well preserved, articulated skeleton of a primitive archaeocetid cetacean from the late Oligocene Yaquina sandstone formation of the central-Oregon coast range. In addition to his described specimen, Emlong mentions two other skulls and partial skeletons of archaeocetid cetaceans from elsewhere in the Yaquina and in the middle Oligocene Toledo Formation in Oregon.

Cetacean diversity in the world Oligocene is strikingly low. Romer (1966) reports only five genera in the Oligocene and more than three times that number in the preceding Eocene, with 138 and 40 genera, respectively, in the succeeding Miocene and Pliocene.

The cetacean described in this report is very similar to the specimen described and named by Emlong (1966) and occurs at what may be close to, if not the same, stratigraphic interval. Several check lists and notes appear in the literature on the molluscs and fossil plants in the rocks bearing the cetacean material described herein. Despite the richness of the invertebrate fossils no systematic study of this material has been effected and it is difficult to establish with precision the stratigraphic position of our cetacean locality.

Locality

Nine vertebrae were recovered from an exposure in the bed of Butte Creek where it forms the Clackmas/Marion County line approximately 25 miles northeast of Salem in township 6 South, Range 2 East, section 29, about 100 yards east of the western boundary of section 29 (Fig. 1). The silicified bone occurs in a matrix of well-indurated tufaceous siltstones, and several of the vertebrae have been distorted. Associated with the cetacean fossils are pieces of carbonized wood and worn fragments of molluscan shell material.

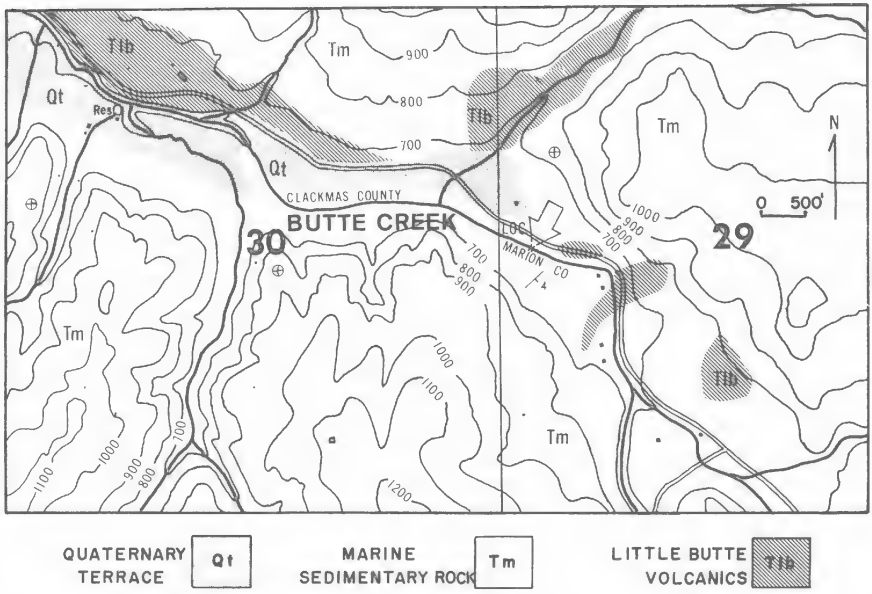


Figure 1. Geologic map of the Upper Butte Creek area showing location of collecting site (modified from Hampton, 1972).

Sandstones and siltstones of the "Butte Creek Beds" are relatively flatlying regionally but dip about five degrees to the southeast in the immediate vicinity of the fossil locality.

Correlations with Regional Geology

Several early papers (Washburn, 1914; Thayer, 1939; O'Neill, 1939; Treasher, 1942) deal with various aspects of the regional geology of the western Cascades. One of the first specific studies of geology in the immediate area of the locality described here was that of Harper (1946), wherein he designated the informal term "Butte Creek Beds." These beds were described as several hundred feet of marine and terrestrial sedimentary rocks exposed in the area of Marquam, Butte Creek and Abiqua Creek of Northern Marion County.

Regionally, the marine clastics of the Butte Creek Beds form a small portion of the eastern margin of a seaway (Fig. 2) that covered a large area in northwest Oregon and western Washington. This seaway persisted from Eocene through late Oligocene time (Snavely, Wagner and McCloud, 1969) and is marked by intermittent regression of the strand line. Volcanic activity contributed tufaceous silts and sands to the marine sedimentary basin to the west, while plant material on the coastal plain accumulated in sufficient quantities to form local beds of lignitic coal.

Much of the difficulty of correlating the Butte Creek Beds with other units in the western Cascades, Willamette Valley and Coast Range lies in the genetic similarity of this unit to several other units of variable age in the Pacific Northwest.

Marine molluscs, as well as fossil leaves from the Butte Creek Beds, have been

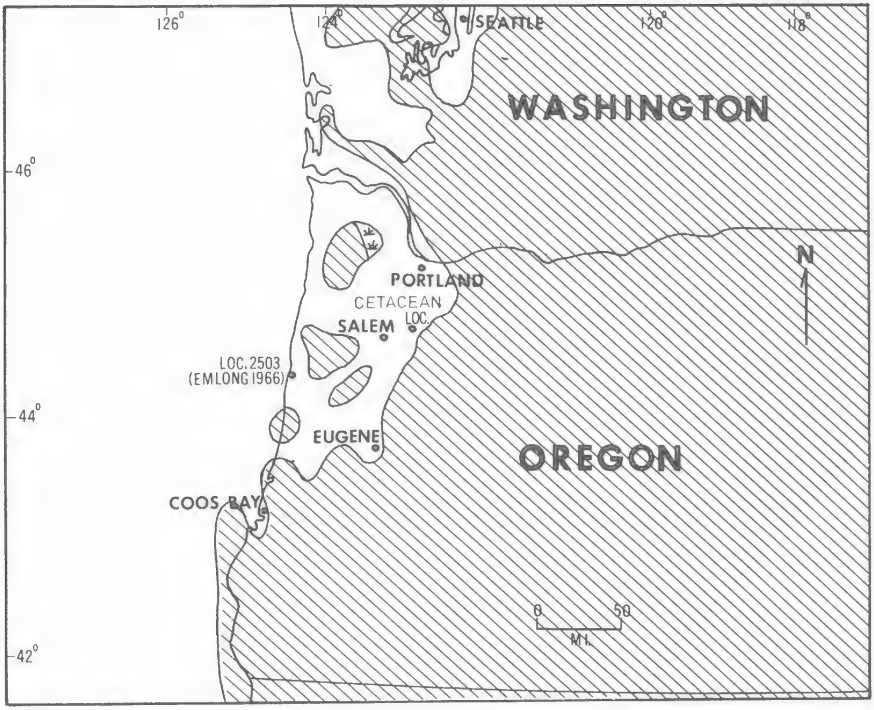


Figure 2. Oligocene paleogeography in Oregon and Washington (after Snavely and Wagner, 1963).

mentioned briefly by Durham and others (1942) and were compared to the Vaqueros faunas of California and the Eagle Creek flora of Oregon. On the basis of these comparisons, Durham and others assigned the Butte Creek Beds to the lower Miocene.

Peck and others (1964) mapped a large area in the western Cascades of Oregon. In their report, they regarded the Butte Creek Beds of Harper (1946) as lower Miocene to upper Oligocene. The latter correlation was made on the basis of invertebrate faunas described by Vokes and Warren (1951). The invertebrate assemblage from the Butte Creek Beds noted by Harper (1946), as well as that collected by the present authors, is similar but not identical to the Oligocene Eugene Formation fauna reported by Hickman (1969) (Table 1).

The most recent work in the area by Hampton (1972) deals primarily with the

TABLE 1. Molluscs occurring in the Butte Creek Beds and the Eugene Formation.

Pelecypods	Gastropods
Acila shumardi (Dall)	*Epitonium condoni* (Dall)
Nuculana washingtonensis (Weaver)	*Calyptraea diegoana* (Conrad)
Lucinoma acutilineata (Conrad)	*Polinices washingtonensis* (Weaver)
Pitar clarki (Dickerson)	*Exilia lincolnensis* (Weaver)
Spisula pittsburgensis (Clark)	
Thracia condoni (Dall)	

groundwater resources of the western Cascades and north Willamette Valley. He refers to the rocks in the Butte Creek area informally as "Oligocene and Miocene marine sedimentary rocks" (Hampton, 1972, p. 34) and suggests that the Butte Creek Beds intertongue with and are partially correlative with the Little Butte Volcanics (Fig. 3). Hampton further notes that both the Butte Creek Beds of Harper (1946) and the Illahe formation of Thayer (1939) have been lithologically associated with rocks assigned to the Eugene Formation by Allison and Felts (1956) and Vokes, Snavely, and Myers (1951). Elsewhere, Baldwin (1964) and Hickman (1969) have demonstrated considerable evidence of a middle Oligocene age for the Eugene Formation.

Emlong's (1966) aetiocetid specimen was recovered from a locality near the top of the Yaquina Formation in Lincoln County, Oregon. He regards the Yaquina at that locality as uppermost Oligocene and bases this correlation on a large collection of molluscs collected and described by Vokes and others (1949). Baldwin (1964) has indicated that the Oligocene/Miocene boundary in the central-Oregon coast area occurs within the Yaquina Formation and Peck and others (1964) combined the Yaquina and Scappose Formations into the interval spanning the same boundary. The latter authors also noted a lithologic similarity between the Butte Creek Beds and the middle Oligocene Eugene Formation but regarded the Butte Creek Beds as Scappose Formation equivalents. Baldwin (1964) correlated the Scappose Formation of Northwest Oregon in part with the Yaquina and placed the Oligocene/Miocene boundary

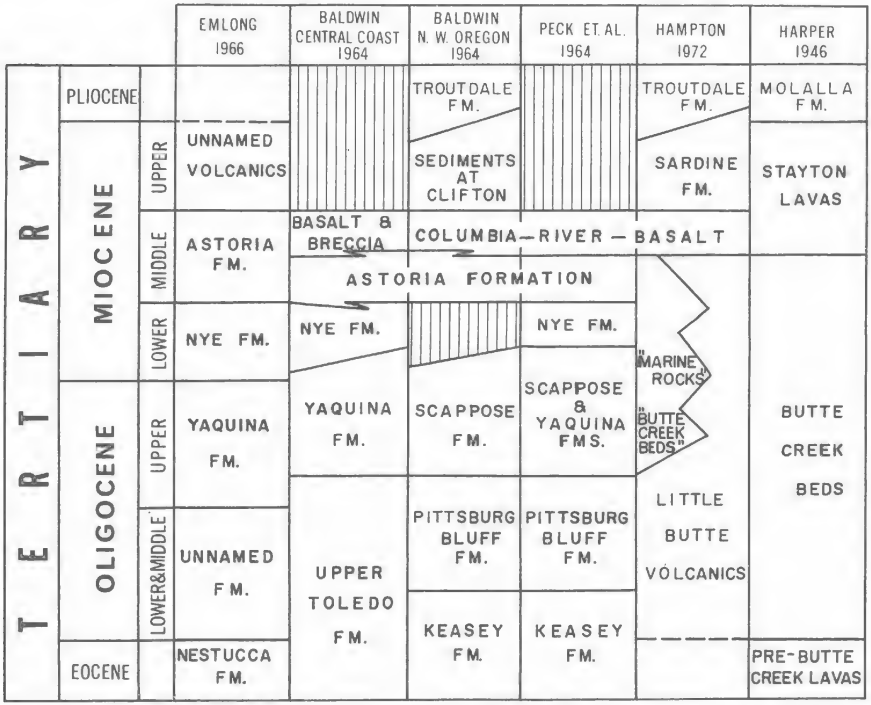


Figure 3. Oligocene and Miocene correlations in the Pacific Northwest.

within the former unit. Although some of the upper portions of the Butte Creek Beds may be early Miocene in age, the best estimate of that interval bearing the cetacean fossil seems to be late Oligocene.

The abundance of water-worn mollusc and barnacle fragments in these sediments in the immediate vicinity of the cetacean locality, as well as the inculcation of fossilized wood and leaves with the marine invertebrates, clearly indicates a strand paleoenvironment.

Discussion

The low diversity of Oligocene cetaceans as compared to cetacean faunas of the Miocene and Eocene merits attention here. Because the distribution and number of extant cetaceans corresponds closely with that of marine plankton, it is useful to examine the fossil record of the plankton that comprise Oligocene marine assemblages. Lipps (1970) has compared the diversities of several groups of fossil marine plankton, including: calcareous nannoplankton, dinoflagellates, silicoflagellates, diatoms, ebridians, and planktonic foraminifera. He has demonstrated a greatly diminished or waning diversity for each of these groups during the Oligocene epoch. Lipps has proposed a thermally controlled model to explain this fluctuation in plankton diversity. The basis of his model is that cool periods cause the establishment of vertical and lateral biologic thermal barriers in the oceans. These barriers induce biologic isolation and subsequent high plankton diversities. Warm periods create thermally homogeneous oceans with subsequent mixing and low diversity regimes. On the strength of this model, the Oligocene would be interpreted as a warm interval characterized by low plankton diversity.

Although it is impossible to demonstrate conclusively a relationship between these plankton and cetacean-diversity lulls in the Oligocene, the curve similarity (Fig. 4) for these two parameters is remarkable.

Systematics

Order Cetacea
Suborder Archaeoceti
Family Aetiocetidae Emlong
Genus *Aetiocetus* Emlong
Aetiocetus cf. cotylalveus Emlong

Fossil specimens consist of nine silicified vertebrae preserved articulated (Fig. 5). The vertebrae were lying on their right side where they were exposed in the stream bed, and most of the transverse processes and metapophyses on the left side of the three posterior-most (caudal) vertebra were destroyed by erosion. The remainder of these, and the rest of the vertebrae, are present, but several are crushed laterally. Illustrations of vertebrae presented here are all reconstructions.

Much of the justification for the establishment of the family Aetiocetidae is implicit in skull structures described in detail by Emlong (1966). Although we lack skull remains, our vertebral specimens are very similar to those reported by Emlong. On the basis of comparison with Emlong's illustrations, the Butte Creek cetacean remains appear to comprise the eighth through the tenth lumbar vertebrae and the first through the sixth caudals. No other cetacean fossil material was recovered from the Butte Creek site, and the skeleton apparently was partially disarticulated prior to burial.

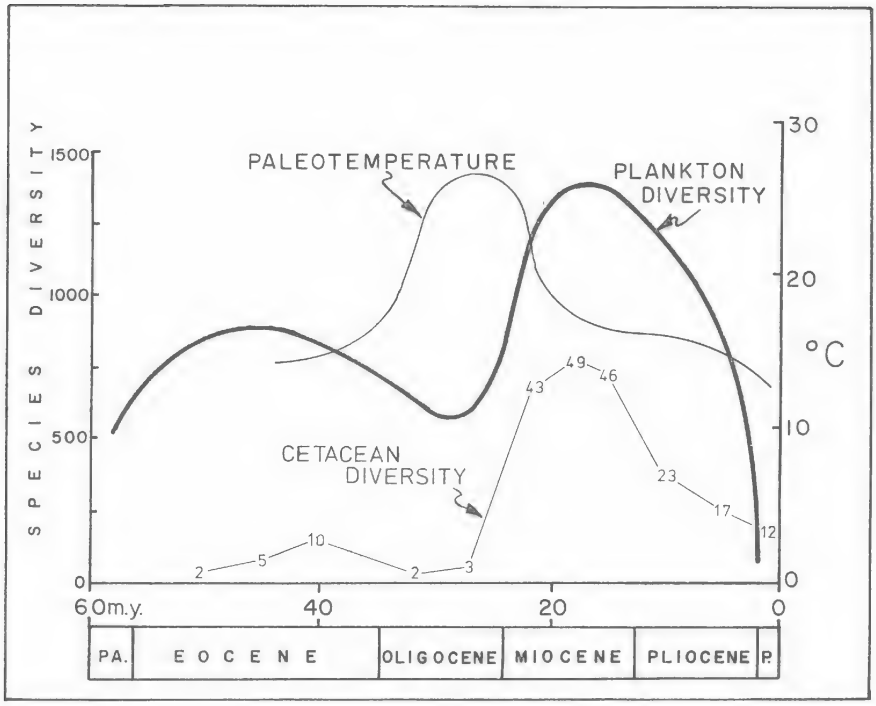


Figure 4. Tertiary paleotemperature, plankton diversity, and cetacean diversity (number of genera). (Modified from Dorman, 1968; Lipps, 1969; and Romer, 1966.)

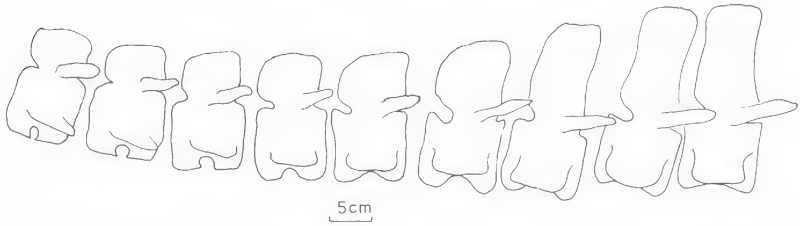


Figure 5. Reconstruction of vertebrae. Right lateral view. From right to left: *8th* through *10th* lumbars and *1st* through *6th* caudals.

Lumbar Vertebrae

The three lumbar vertebrae are very similar. These vertebrae display a vertical to slightly posteriorly directed neural spine which is antero-posteriorly broad, particularly at the distal end. The neural arch is low. Transverse processes are crushed flat into the plane of the neural spine, and all of these processes are broad antero-posteriorly in a spatulate fashion. The forward projection on the transverse process described by Emlong is present on our specimen only on the ninth lumbar. No transverse processes of any of the vertebrae bear foramina. Antero-posterior length at the centrum of all

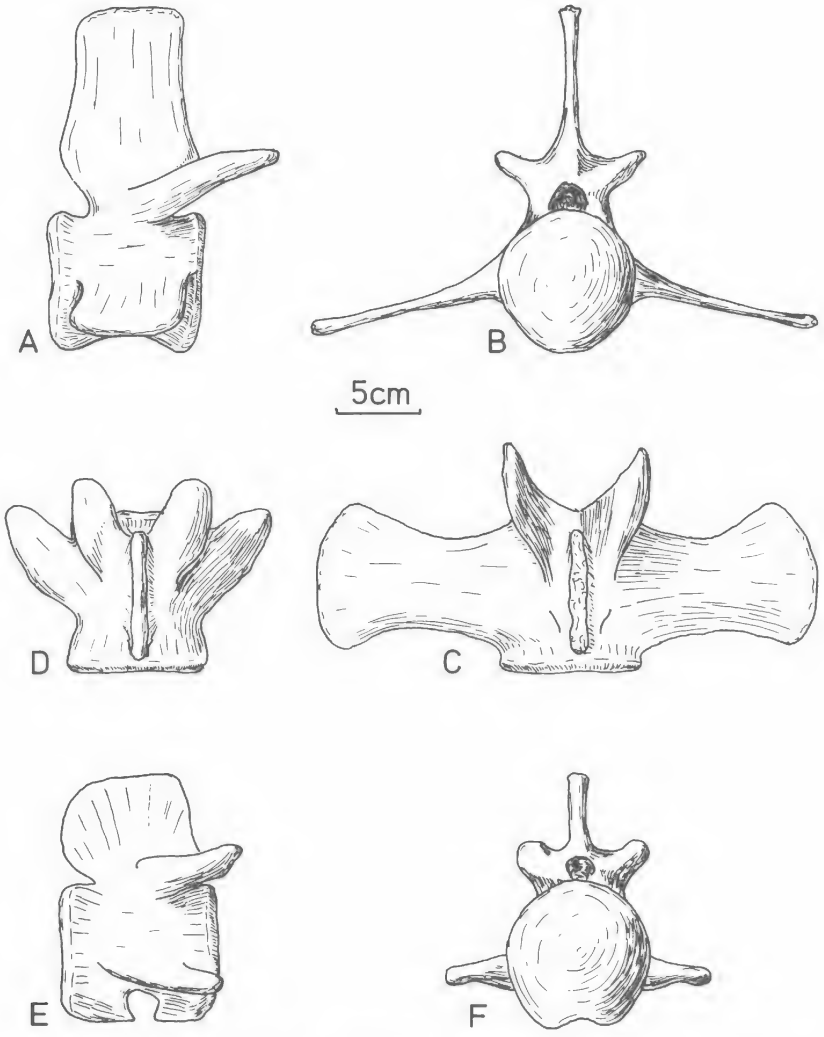


Figure 6. Reconstructed vertebrae. Eighth lumbar—A. Right lateral view. B. Posterior view. C. Dorsal view. Fifth caudal—D. Dorsal view. E. Right lateral view. F. Anterior view.

three lumbars averages 90 mm, but this and other measurements have been affected by crushing. The anterior and posterior centrum faces average 85 mm in diameter, and the greatest total vertical height averages 190 mm. Metapophyses are well developed and extend anteriorly up to 30 mm beyond the center.

Caudal Vertebrae

Neural spines diminish in height rapidly from 80 mm in the first caudals to 40 mm in

the sixth. The forward rake of the neural spine is diminished posteriorly and the spine continues to maintain a broad rounded crest. Transverse processes diminish in length toward the posterior caudals and attain a strong anterior projection in the fifth and sixth caudals. Chevron facets become progressively pronounced toward the posterior end of the caudal series. The antero-posterior length of the caudals and the diameter of the centrum faces both average 85 mm. Total vertical height decreases with the second caudal and averages 150 mm for the second through the sixth caudals. Metapophyses are progressively reduced in size toward the rear of the series.

Acknowledgements

The writers express their appreciation to Dr. E. M. Baldwin for manuscript suggestions. F. B. Fryberger is thanked for permission to collect the fossil specimens on his property. The senior author's 1972 summer paleontology class is acknowledged for its collective assistance in extracting and recovering fossil specimens from the collecting site.

Literature Cited

Allison, I. S., and Felts, W. M. 1956. Reconnaissance geologic map of the Lebanon Quadrangle, Oregon. Oregon Dept. Geol. & Min. Indust. Map with text.
Baldwin, E. M. 1964. Geology of Oregon, 2nd ed. Eugene, Oregon, 165 p.
Condon, T. 1906. A New Fossil Pinniped (*Desmato phoca oregonensis*) from the Miocene of the Oregon coast. Bull. Univ. of Ore., vol. 3, no. 3, pp. 5-14.
Dorman, F. H. 1968. Some Australian Oxygen Isotope temperatures and a theory for a 30 million year temperature cycle. J. Geol., vol. 76, pp. 297-313.
Durham, J. W., Harper, H. E., and Wilder, B. 1942. Lower Miocene in the Willamette Valley Oregon. (abs.) Geol. Soc. Amer. Bull., vol. 53, no. 12, pt. 2, p. 1817.
Emlong, D. R. 1966. A New Archaic Cetacean from the Oligocene of Northwest Oregon. Univ. of Ore. Mus. of Nat. Hist. Bull., no. 3, pp. 1-51.
Hampton, E. R. 1972. Geology and Ground Water of the Molalla—Salem Slope Area, Northern Willamette Valley, Oregon. U.S.G.S. Water Supply Paper 1997, 83 p.
Harper, H. E. 1946. Preliminary Report on the Geology of the Molalla Quadrangle, Oregon. Unpublished master's thesis, Oregon State Univ.
Hickman, C. J. 1969. The Oligocene Marine Molluscan Fauna of the Eugene Formation in Oregon. Univ. of Ore. Mus. of Nat. Hist. Bull., no. 16, 112 p.
Lipps, J. H. 1970. Plankton Evolution. Evolution, vol. 24, no. 1, pp. 1-22.
O'Neill, T. F. 1939. The Geology of the Stayton Quadrangle, Oregon. Corvallis. Oregon State Coll., unpublished master's thesis, 83 p.
Packard, E. L., and Kellog, A. R. 1934. A Cetothere from the Miocene Astoria Formation at Newport, Oregon. Publ. Carn. Wash., no. 447, pp. 1-62.
Peck, D. L., Griggs, A. B., Schlicker, H. G., Wells, F. G., and Dole, H. M. 1964. Geology of the Central and Northern Parts of the Western Cascade Range in Oregon. U.S.G.S. Prof. Paper 449.
Romer, A. S. 1966. Vertebrate Paleontology. Univ. of Chicago Press, 687 p.
Snavely, P. D., Jr., and Wagner, H. C. 1963. Tertiary Geologic History of Western Oregon and Washington. Wash. Div. of Mines and Geol. Rept. Inv. 22, 25 p.
Thayer, T. P. 1939. Geology of the Salem Hills and the North Santiam River basin, Oregon. Ore. Dept. Geol. and Min. Indust. Bull. 15, 40 p.
Treasher, R. C. 1942. Geologic Map of the Portland area, Oregon, with Text on back. Ore. Dept. Geol. & Min. Indust.
Vokes, H. E., Norbisrath, H., and Snavely, P. D. 1949. Geology of the Newport-Waldport area, Lincoln County Oregon. U.S.G.S. Oil and Gas Inventory prelim. map no. 83.
Vokes, H. E., Snavely, P. D., and Myers, D. A. 1951. Geology of the Southern and Southwestern border areas, Willamette Valley, Oregon. U.S.G.S. Oil and Gas Inv. Map OM-110 geol. map and text.
Washburne, C. W. 1914. Reconnaisance of the Geology and Oil Prospects of Northwestern Oregon. U.S.G.S. Bull. 590, 111 p.

Received April 19, 1974.
Accepted for publication April 28, 1975.

Grant A. Harris
Dept. For. & Range Mgt.
Washington State Univ.
Pullman, WA 99163

Northwest Science

W. H. Rickard

Ecosystems Department
Battelle Memorial Institute
Pacific Northwest Laboratories
Richland, Washington 99352

Litterfall in a Douglas-Fir Forest near the Trojan Nuclear Power Station, Oregon[1]

Abstract

Litterfall in a second growth Douglas-fir forest was estimated at 3.43 metric tons per hectare per year. Fifty-eight percent was Douglas-fir leaves, 17 percent broad leaves, 9 percent female cones of Douglas-fir, 7 percent small twigs, and 9 percent miscellaneous fragments. Litterfall was a continuous process, but more litterfall occurred in summer and autumn than other seasons of the year. Broad leaves were richer in macro- and micronutrient elements than Douglas-fir leaves. The annual contribution of macronutrients N, P, K, Mg, Ca, and S in leaf-fall was 82 kg per hectare.

Introduction

Douglas-fir, *Pseudotsuga menziesii,* is the most widespread and valuable lumber tree in western Oregon and Washington; and it is important at the Trojan nuclear power station because it dominates plant communities, provides habitat for wildlife, and adds aesthetic beauty to the landscape. Douglas-fir communities also provide biological material useful for study of long-term effects of power-station operation, especially the fate of dissolved minerals in water droplets released from the operating cooling tower.

The purpose of this investigation was to measure the amount and composition of litterfall and its mineral content for a year prior to the operation of the Trojan station and also to provide additional information concerning mineral cycling behavior of western Douglas-fir forests.

The Site

The Trojan nuclear power station is located on the west bank of the Columbia River near Prescott, Columbia County, Oregon. Well-drained slopes support Douglas-fir forests and wet soils support deciduous trees, especially black cottonwood, *Populus trichocarpa,* and Oregon ash, *Fraxinus latifolia.* The forest is interrupted by ponds and marsh habitats dominated by reed canary grass, *Phalaris arundinacea,* and willows, *Salix* spp. A few acres support pasture grasses which are maintained by annual cuttings. The power station and ancillary support facilities occupy about 40 acres on an 800-acre site.

The regional climatic pattern is shown in Table 1 as reported from the Longview, Washington weather station.

[1] Work performed for Portland General Electric Company, Portland, Oregon, as a part of a terrestrial ecology baseline study for the Trojan Nuclear Power Station.

TABLE 1. Average precipitation and temperature for the Longview, Washington, weather station 1931-1960.

Month	Ppt (cm)	Max. temp. (C)	Min. temp. (C)
Jan	14.7	7	0
Feb	12.4	9	1
Mar	12.3	12	2
Apr	6.9	16	4
May	5.8	20	6
Jun	5.3	22	9
Jul	2.0	26	10
Aug	3.3	25	11
Sep	5.1	23	9
Oct	11.2	17	6
Nov	16.3	11	3
Dec	19.3	8	1
Year (Total)	114.6	(Avg.) 17	(Avg.) 5

Methods Employed

Two plots, each 15 x 30 meters, were staked out in a 60-acre forest located immediately north of the cooling tower. The living trees in each plot were counted and trunk circumferences measured at breast height. Basal area of trunks were later calculated from these circumference measurements.

Litterfall collection devices were improvised from circular, plastic kitchen colanders, each 0.0356 m^2. The colanders were fastened to wooden stakes to prevent animals from dislodging them. A plastic screen of fine mesh was cut to fit the colander bottom. The screen expedited removal of collected litter and prevented fragments of litterfall from passing through the colander holes and yet let rainfall drain through.

Litterfall collectors were located in eight groups of five, each group centered on a randomly selected point inside each study plot. Four collectors were located systematically from the random point forming the four corners of a square with the random point in the center. Adjustments were made to avoid fallen logs and tree trunks.

Initial placement of collectors was near the ground. Later the collectors were elevated 3-4 decimeters above ground level supported on wooden stakes. This procedure was necessary to prevent blackberry vines from overgrowing the collectors.

Animals, mostly deer, occasionally dislodged or damaged the collectors; therefore, litterfall collections were lost from some collection periods. Litterfall was gathered six times between 15 May 1972, and 8 December 1973. Annual litterfall was, therefore, based on the values obtained between September 1972 and September 1973.

Litterfall from each colander was hand separated into five categories: (1) Douglas-fir leaves; (2) broad leaves; (3) cones; (4) small twigs; and (5) miscellaneous, all dried at 50°C for 48 hours in a forced-air oven and weighed following each collection date. A sample of each category was prepared by grinding the entire collection from each plot in a Wiley mill. Broad-leaf and Douglas-fir leaf categories were chemically analyzed by the United States Testing Company, Richland, Washington.

Total nitrogen was determined using the micro-Kjeldahl procedure on oven-dry plant tissues. Potassium, calcium, magnesium, sodium, iron, manganese, barium, boron, copper, zinc, and molybdenum were analyzed on ashed samples using atomic absorption procedures. Phosphorus was analyzed colorimetrically, employing the ammonium molyb-

date-stannous chloride procedure, and sulfur was determined using the magnesium nitrate method as outlined in the official methods of analysis of the Association of Official Agricultural Chemists (1965).

Results

Douglas-fir trees dominated the overstory in both study plots. Twenty-two Douglas-fir trees occurred on plot number one and 16 on plot number two (Table 2). Bigleaf maple and Oregon oak were sparingly represented. The Douglas-fir trees ranged in size from 13 to 48 cm in diameter and averaged 33 cm. Plot number two had fewer fir trees and less basal area than did plot number one. The largest trees were estimated at 60 years of age judging from examination of wood cores taken with an increment borer. Tree heights were not measured, but some trees were estimated to be 20 meters tall.

TABLE. 2. Density units and basal area (m^2) of living trees on two 450 m^2 plots in a Douglas-fir forest at the Trojan nuclear power station, Oregon.

	Number		Basal Area (m^2)	
Species	Plot 1	Plot 2	Plot 1	Plot 2
Douglas-fir	22	16	2.25	1.45
Bigleaf maple	1	1	0.09	0.01
Oregon oak	0	3	0	0.03
Total	23	20	2.34	1.5

The understory consisted mainly of deciduous shrubs, especially California hazel, *Corylus cornuta;* ocean spray, *Holodiscus discolor;* red currant, *Ribes sanguineum;* and buckbrush, *Ceanothus sanguineus.* Blackberry vines, *Rubus ursinus,* and honeysuckle, *Lonicera ciliosa,* were locally abundant.

Annual Litterfall

The total litterfall collected between September 1972 to September 1973 averaged 343 g m^{-2} or 3.43 metric tons per hectare (Table 3). Overall, 58 percent of the litterfall consisted of Douglas-fir leaves, 17 percent consisted of broad leaves from deciduous trees and understory shrubs, 9 percent consisted of Douglas-fir cones, and the remainder was small twigs and miscellaneous fragments of bark, male cones, fragments of female cones, and detritus.

TABLE 3. Annual litterfall, September 1972 to September 1973, expressed as gm^{-2} at four sampling periods at the Trojan nuclear power station.

Litterfall category	28 Sep-15 Nov-1972	16 Nov-25 Jan-1973	26 Jan-15 May-1973	16 May-18 Sep-1973	Total	Percent of total
Douglas-fir leaves	93	17	18	70	198	58
Broad leaves	27	14	4	12	57	17
Cones	6.5	7.5	9	7.5	30	9
Small twigs	5	4.5	6	10	26	7
Miscellaneous	5.5	2.5	2.5	22	32	9
Total	137	45	39	121	343	100

Litterfall was a continuous process, but more was collected during the dry summer and autumn months than in the moist winter and spring seasons (Table 3). In autumn, litterfall averaged 2.8 g m^{-2} day^{-1} over a 48-day period, but only 0.37 g m^{-2} day^{-1} during a 109-day period in winter.

Mineral Content of Fallen Leaves

On the average, leaves of deciduous trees and shrubs had higher concentrations of nitrogen, phosphorus, potassium, magnesium, calcium, sodium, and sulfur than did the leaves of Douglas-fir (Table 4). They also had higher average concentrations of iron, manganese, barium, boron, copper, zinc, and molybdenum.

TABLE 4. Average values (± standard error) of macro- and micronutrient concentration in Douglas-fir leaves and broad leaves collected as litterfall at the Trojan nuclear power station, 1972-1973.

Macronutrients and sodium	Broad leaves	Douglas-fir leaves	Micronutrients	Broad leaves	Douglas-fir leaves
	percent dry wt.			ppm	
N	1.34 ± .25	1.01 ± .14	Fe	505 ± 57	168 ± 9
P	0.27 ± .09	0.10 ± .02	Mn	352 ± 40	136 ± 13
K	0.26 ± .08	0.12 ± .03	Ba	34 ± 7	24 ± 2
Mg	0.19 ± .03	0.07 ± .01	B	34 ± 3	18 ± 2
Ca	2.10 ± .12	1.41 ± .08	Cu	19 ± 5	7.6 ± 2
Na	0.08 ± .01	0.04 ± .01	Zn	52 ± 6	21 ± 7
S	0.16 ± .01	0.11 ± .01	Mo	1.1 ± 0.4	0.8 ± 0.1

The amount of nitrogen (N); phosphorus (P); potassium (K); magnesium (Mg); calcium (Ca); sodium (Na); and sulfur (S) contributed to the forest floor as fallen leaves per m^2 was 8.2 grams per year (Table 5). About 5.7 grams were contributed in Douglas-fir leaves and 2.5 grams as broad-leaf species. Calcium was the most abundant of the seven mineral elements, followed in decreasing order of abundance by N>K>P>S>Mg>Na. The total macronutrient contribution was 82 kg per hectare per year associated with 2.55 metric tons of leaf fall.

TABLE 5. Annual mineral fall in Douglas-fir and broad leaves expressed as grams per square meter of forest floor at the Trojan power station 1972-1973.

Macronutrients and sodium	Douglas-fir leaves	Broad leaves	Total
N	2.0	.76	2.76
P	.20	.15	.35
K	.24	.15	.39
Mg	.14	.11	.25
Ca	2.8	1.2	4.00
Na	.079	.045	.12
S	.21	.091	.30
Total	5.67	2.51	8.18

Statistics of Litterfall Collections

The area sampled by 40 litterfall collectors was 1.4 m^2. It was anticipated that the collectors would be most efficient in sampling the small but numerous Douglas-fir

leaves and less efficient at collecting larger deciduous leaves, cones, and small twigs.

To show the variation between plots and between sampling periods, the coefficients of variation (C.V.), the value obtained by dividing the standard deviation by the mean, are shown (Table 6). The average C.V. was smallest for the Douglas-fir leaf category, followed by total litterfall, broad leaves, miscellaneous, small twigs, and finally cones. The average C.V. was nearly identical for Douglas-fir leaves in either plot.

It was necessary to separate the litterfall into categories because of expected differences in chemical composition of different plant parts and between broad leaves and Douglas-fir leaves.

Discussion

In the absence of logging, wildfire, and insect infestation, the stand of Douglas-fir trees at the Trojan site can be expected to persist throughout the operating life of the power station, i.e., 30-40 years, providing that salt and heavy metals deposited as drift droplets are not harmful to tree growth. This investigation provides data showing the mineral content of Douglas-fir and broad leaves, and also measures the amount of litter falling to the forest in a year prior to the start up of the nearby nuclear power station. Follow-up studies conducted after the station becomes operational will permit a measurement of changes in the mineral content and/or changes in the amount of litterfall as related to power station operations.

The amount of annual leaf fall depends upon stand density, tree age, and vigor. As the trees age, understory shrubs will tend to become less vigorous as the scarce essential nutrient elements in the soil become bound in wood and as the expanding tree canopies provide more complete ground shade. As the trees senesce, leaf production tends to lessen and the trees themselves become more susceptible to damage by insect pests, disease, ice, wind, and snow damage.

The amount of litterfall at the Trojan site is similar to the average values obtained for conifer forests in other geographic areas (Bray and Gorham, 1963). Cole and Dice (1969) measured the annual return of macronutrients to the forest floor of a 36-year-old Douglas-fir plantation in western Washington and obtained a value for nitrogen at 13.6 kilograms per hectare per year. Phosphorus, potassium, and calcium values were 0.2, 2.7, and 11.1, respectively. Douglas-fir leaves at the Trojan sites returned 20 kg of nitrogen, 2.0 kg of phosphorus, 2.4 kg of potassium, and 28 kg of calcium per hectare per year. Calcium values at the Trojan site were twice those of the Washington site.

Daubenmire (1953) measured N, P, K, and Ca in freshly fallen Douglas-fir leaves in northern Idaho forests where values averaged 0.60, 0.13, 0.49, and 1.57 percent by dry weight, respectively. The average percent contents of these same elements in fallen leaves at Trojan were 1.01 (N), 0.10 (P), 0.12 (K), and 1.40 (Ca). The nitrogen content of Trojan samples was higher than that of the Idaho samples; however, phosphorus and calcium levels were similar.

Cooling-tower effluents are recent additions to atmospheric burdens, and data are not readily available concerning the fate and biological effects of metal ions associated with cooling-tower drift. Studies conducted at an operating experimental cooling tower at Oak Ridge, Tennessee, showed that mineral constituents of drift were highest in wild plants growing close to the tower (Taylor et al., 1974). Mineral concentra-

TABLE 6. Average litterfall, grams dry weight per collector, in two forest plots at the Trojan nuclear power station for six collection periods, 1972-1973, and coefficient of variation ( ).

Date	Douglas-fir leaves	Broad leaves	Cones	Small twigs	Misc.	Total
			Plot One			
Sep (n = 40)	1.9 (.17)	.24 (1.6)	.92 (2.7)	.16 (2.6)	.32 (1.2)	3.5 (0.82)
Nov (n = 40)	4.1 (.18)	.32 (1.2)	.40 (3.6)	.20 (1.8)	.12 (1.9)	5.1 (0.33)
Jan (n = 40)	0.48 (.70)	.41 (0.91)	.29 (0.95)	.09 (1.5)	.06 (2.7)	1.3 (1.0)
May (n = 40)	0.59 (.36)	.15 (0.92)	.49 (3.6)	.24 (1.4)	.08 (2.3)	1.5 (1.2)
Sep (n = 39)	2.2 (.72)	.14 (1.1)	.53 (3.5)	.26 (1.3)	.80 (0.53)	3.9 (0.68)
Dec (n = 40)	2.9 (.24)	.73 (1.3)	.20 (6.3)	.25 (1.6)	.28 (0.74)	4.4 (0.49)
Average	2.0 (.39)	.33 (1.2)	.47 (3.4)	.20 (1.7)	.28 (1.6)	3.3 (0.75)
			Plot Two			
Sep (n = 31)	3.7 (.32)	1.3 (0.58)	.36 (4.2)	.44 (3.6)	.65 (0.68)	6.4 (0.46)
Nov (n = 31)	2.5 (.46)	1.6 (0.68)	.08 (5.6)	.14 (1.5)	.30 (0.92)	4.6 (0.47)
Jan (n = 31)	0.75 (.37)	0.60 (0.89)	.25 (5.6)	.22 (1.6)	.10 (1.1)	1.9 (0.94)
May (n = 30)	0.71 (.38)	0.13 (2.3)	.12 (5.5)	.18 (1.4)	.12 (1.3)	1.3 (0.66)
Sep (n = 31)	2.8 (.26)	0.68 (0.70)	0	.47 (1.2)	.77 (0.32)	4.7 (0.21)
Dec (n = 37)	3.0 (.40)	1.7 (0.60)	.09 (6.1)	.13 (2.1)	.42 (0.69)	5.3 (0.35)
Average	2.2 (.36)	1.0 (0.96)	.15 (5.4)	.26 (1.9)	.39 (0.83)	4.0 (0.51)

tions of plant foliage declined exponentially with increasing distance from the tower. There were no apparent morphological aberrations that could be attributed to drift deposition upon wild plants.

Literature Cited

Abee, A., and D. P. Lavender. 1972. Nutrient cycling within old-growth Douglas-fir stands, pp. 133-144. In: *Research on Coniferous Forest Ecosystems,* J. Franklin, L. J. Dempster, and R. H. Waring (eds.). USDA Forest Service, Portland. 322 pp.

Antonovics, J., A. D. Bradshaw, and R. G. Turner. 1971. Heavy metal tolerance in plants. *Adv. in Ecological Res.* 7: 1-85.

Association of Official Agricultural Chemists. 1955. *Official Methods of Analysis.* Tenth ed. Washington, D.C. 957 pp.

Bray, J. R., and E. Gorham. 1964. Litter production of forests of the world. *Adv. in Ecol. Res.* 2: 101-152.

Cole, D. W., and S. F. Dice. 1969. Biomass and nutrient flux in coniferous forest ecosystems: The development of a quantitative ecological approach, pp. 55-67. In: *Coniferous Forests of the Rocky Mountains.* Proceedings of 1968 symposium, Univ. of Montana, Missoula.

Daubenmire, R. 1953. Nutrient content of leaf litter of trees in the northern Rocky Mountains. Ecology 34: 786-793.

Taylor, F. G., Jr., L. K. Mann, R. C. Dahlman, and F. L. Miller. 1974. Environmental effects of chromium and zinc in cooling water drift. Proceedings of the Cooling Tower Environmental Symposium, AEC Conf. 740302 sponsored by the AEC and the State of Maryland, Univ. of Maryland.

Received March 26, 1975.
Accepted for publication July 7, 1975.

W. T. McDonough

Plant Physiologist, USDA Forest Service
Intermountain Forest and Range Experiment Station
Ogden, Utah 84401[1]

Germination Polymorphism in Grindelia squarrosa (Pursh) Dunal

Abstract

Disc and ray achenes of *Grindelia squarrosa* (Pursh) Dunal var. *serrulata* (Rydb.) Steyerm. (curlycup gumweed) differ in their morphology and requirements for germination. Disc achenes germinate more rapidly and attain higher final germination percentages over a broader range of temperatures than do ray achenes. Some achenes of both types have a light requirement for germination, but the proportion is much less in the disc achenes. Low-temperature stratification increases the range of conditions suitable for germination of both types of achenes, but has a greater effect on disc achenes. Over 24-h imbibition, disc achenes attain a higher water content (98%) and a lower water potential (to –25 bars) than ray achenes (75% and –8 bars).

Since growth of isolated embryos of both types occurs under conditions that are inhibitory to the germination of intact achenes, differences in germination are attributed to a thicker pericarp in the ray achenes that impedes embryo growth to a greater extent than does the thin pericarp of disc achenes. Different responses of the two types of achenes probably result in germination and emergence during different seasons, with consequent effects on the time required for completion of the growth cycle.

Seed polymorphism—the production of two or more distinct morphological types of dispersal units by individual plants of a species—is commonly found in forbs, particularly *Chenopodiaceae, Cruciferae,* and *Compositae* (Harper, 1965). In the *Compositae,* the morphological distinction is between disc and ray achenes. These morphological dissimilarities may require different environmental requirements for germination. Achenes of the biennial composite *Grindelia squarrosa* (Pursh) Dunal var. *serrulata* (Rydb.) Steyerm. (curlycup gumweed) show this morphological and germination polymorphism; morphologically distinct disc and ray achenes (Fig. 1) differed in germination rates and totals of three test temperatures (McDonough, 1969). This germination polymorphism and the basis for differences in germination response have now been investigated in more detail.

The three varieties of *Grindelia squarrosa* (*quasiperennis, serrulata, squarrosa*) have aggressively extended their range throughout the western and some midwestern portions of the United States and adjacent parts of Canada (Hitchcock et al., 1955; USDA Forest Service, 1937). Gumweed occurs on disturbed ground and on eroded and overgrazed areas, generally on drier sites. Although most common in the lower elevations of plains and foothills, it is found to 3000 m in Colorado and New Mexico. In northern Utah, it occurs on disturbed ground throughout the valleys and into the adjacent Wasatch Mountains to elevations of at least 2200 m.

[1] Stationed in Logan, Utah, at the Forestry Sciences Laboratory, maintained in cooperation with Utah State University.

Figure 1. Disc (top) and ray (bottom) achenes of gumweed.

Methods

In early fall 1971, achenes were collected from five individual plants growing on disturbed ground near a highway in Tony Grove Canyon (2000 m) on the Cache National Forest in northern Utah. Achenes were bulked into one collection, cleaned, separated into the two types, and stored in vapor-tight bottles at 2 C until used.

Sets of 50 achenes of each type, with four replications per treatment, were used in all experiments unless noted otherwise. Achenes were allowed to imbibe water in 9-cm petri dishes on double discs of Whatman No. 1 filter paper saturated with distilled water. Achenes were incubated in Biotronette growth chambers under conditions that included constant or alternating temperatures in the 30-5 C range, with 8-h photoperiods or constant darkness, as was described by Florez and McDonough (1974).

Dishes under light treatments were examined daily for germination during the first 18 days and on alternate days thereafter until the 30th day, when the experiment was terminated. Rates of germination were expressed as days to start of germination (lag time) and days to 50 percent of final germination (halftime). Statistical significance of differences was evaluated by analysis of variance and Studentized range tests (Goldstein, 1964).

Certain other treatments were applied to characterize further the germination responses. When germination was less than 80 percent after 30 days under the test conditions, embryos of ungerminated achenes were extruded from the surrounding pericarp and endosperm by pressing against the cotyledonary end of an achene with a blunt probe. Isolation was not attempted with achenes under the 30 C and 30 C/25 C treatments because of development of a soft rot that probably killed the embryos. Isolated embryos were placed in fresh dishes and returned to the test regimes for an additional 10 days.

Possible involvement of a low-intensity photoreaction in the germination of intact

achenes was also investigated: sets were exposed to various durations of cool white fluorescent light (100 lm/m^2) after 16-h imbibition in darkness. The dishes were returned to constant darkness for 30 days at 25 C/20 C, a temperature favorable for germination under photoperiodic treatment.

The effect of low-temperature stratification on broadening of the conditions for germination was investigated by holding imbibed achenes at 2 C for 150 days in darkness before transferring them to conditions that were unfavorable for germination of unstratified achenes.

Greenhouse and outdoor (lath house) plantings in 25-cm diameter pots filled with native topsoil were used to compare seedling emergence with germination in petri dishes. Achenes were either scattered over the surface of the soil or buried at a depth of 5 mm in early October. All pots were watered regularly. Emergence counts were made after 30 days, during which time the greenhouse temperatures were 25-20 C (day)/20-15 C (night), and outdoor temperatures at the Forestry Sciences Laboratory in Logan, Utah (1600 m), were 20-10 C (day)/15-5 C (night).

To determine the effect of cold treatment on subsequent growth, seedlings were thinned to four per pot. At this time, plants selected had 8 to 14 rosette leaves. Two pots with disc seedlings and two with ray seedlings were transferred to a coldroom at 2 C for 150 days before being returned to the greenhouse; the remaining four pots were left under greehouse conditions. Outdoor seedlings were left in the open through the winter to the following midsummer.

The water potential of imbibing achenes was determined periodically over a 24-h period with Peltier thermocouple psychrometers in vapor-tight chambers of interior dimensions 15 mm diameter x 4 mm height, as described elsewhere (McDonough, 1974). Varying numbers (a set) of achenes of each type (20 disc and 18 ray achenes in four replications) representing approximately 20 mg air-dry weight and multiples thereof were allowed to imbibe water at 22 C on single discs of 14-mm diameter filter paper wetted with 25μl of distilled water. Multiples of the initial weights were used to obtain differing levels of water availability per achene in different treatments. Achenes were also allowed to imbibe water on filter paper in petri dishes for varying periods so that a range of water contents could be obtained. Sets (20 disc, 18 ray achenes) were blotted surface-dry and enclosed in psychrometer chambers. Water-potential determinations were made after 24 h. Water content was determined gravimetrically before and after ovendrying for 16 h at 100 C. Manipulations involving imbibed achenes were done in a glove box at 100 percent RH.

Information on seedling emergence in the field was obtained in October 1971 and June 1972. At each visit, a circular area (0.5 m radius) around each of five plants was examined for emergent seedlings. Seedlings could be identified as to disc or ray origin only when the pericarp was still attached to cotyledons. The extent of dispersal of achenes by late October was determined by examining 100 capitula, 20 on each of the five plants mentioned above.

Results

Germination in Relation to Temperature and Light. With 8-h photoperiods, germination of disc achenes had broad temperature optima in the range of 25-20 C/20-5 C and 30 C/20-15 C (Fig. 2A). Germination of ray achenes was lower at all temperatures

and had narrower optima of 25-20 C/20-15 C (Fig. 2B). Within the optimum range, temperature level, rather than alternating temperature compared to constant temperature, was more important to promotion of germination. In both types of achenes, germination was greatly reduced or did not occur at temperature extremes of 30 C and 15 C or lower.

Trends in germination percentages of disc achenes in darkness were roughly comparable to those in light, but 30-40 percent lower in the optimum range (Fig. 2C). Exceptions included alternating temperatures involving 30 C, which depressed germination to lower levels. Darkness almost completely inhibited germination of ray achenes (Fig. 2D).

For treatments yielding total germination greater than 10 percent, both lag time and halftime were shorter in disc achenes than in ray achenes (Fig. 3A, B). At optimum temperatures for speed of germination, lag times for disc and ray achenes were 2-4 days and 4-7 days, respectively; the corresponding halftimes were 4-8 days and 7-11 days. Except for treatments involving 30 C, the trend for both types of achenes was toward slower rates with lower temperatures during both photoperiod and dark period, an effect corresponding to that for total germination.

Germination of Isolated Embryos. For both types of achenes, failure to germinate under test regimes was due to the pericarp or endosperm surrounding the embryo or both.

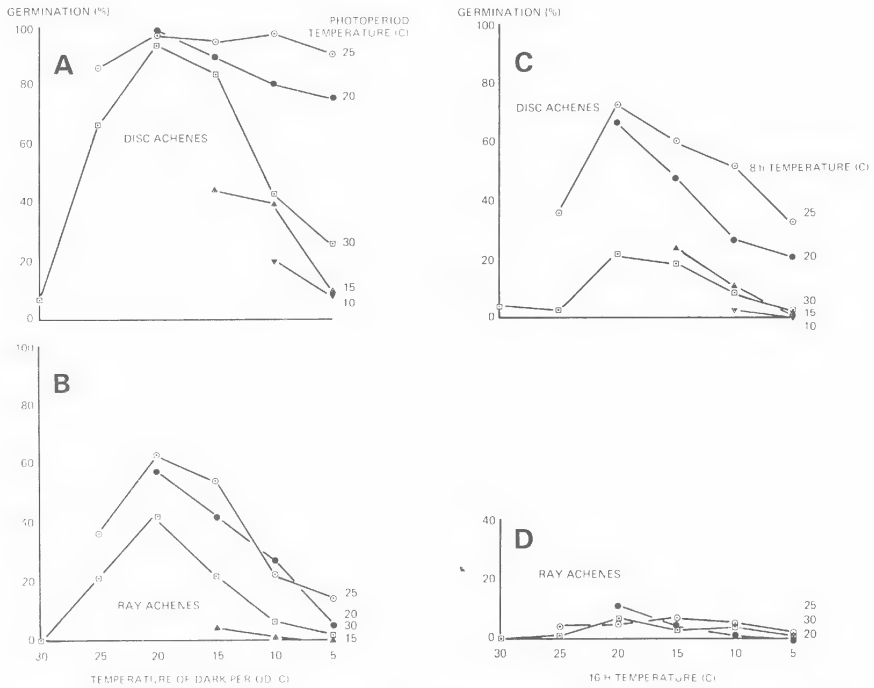


Figure 2. Thirty-day germination percentages of disc and ray achenes at various temperatures with photoperiodic treatment (A, B) and in darkness (C, D).

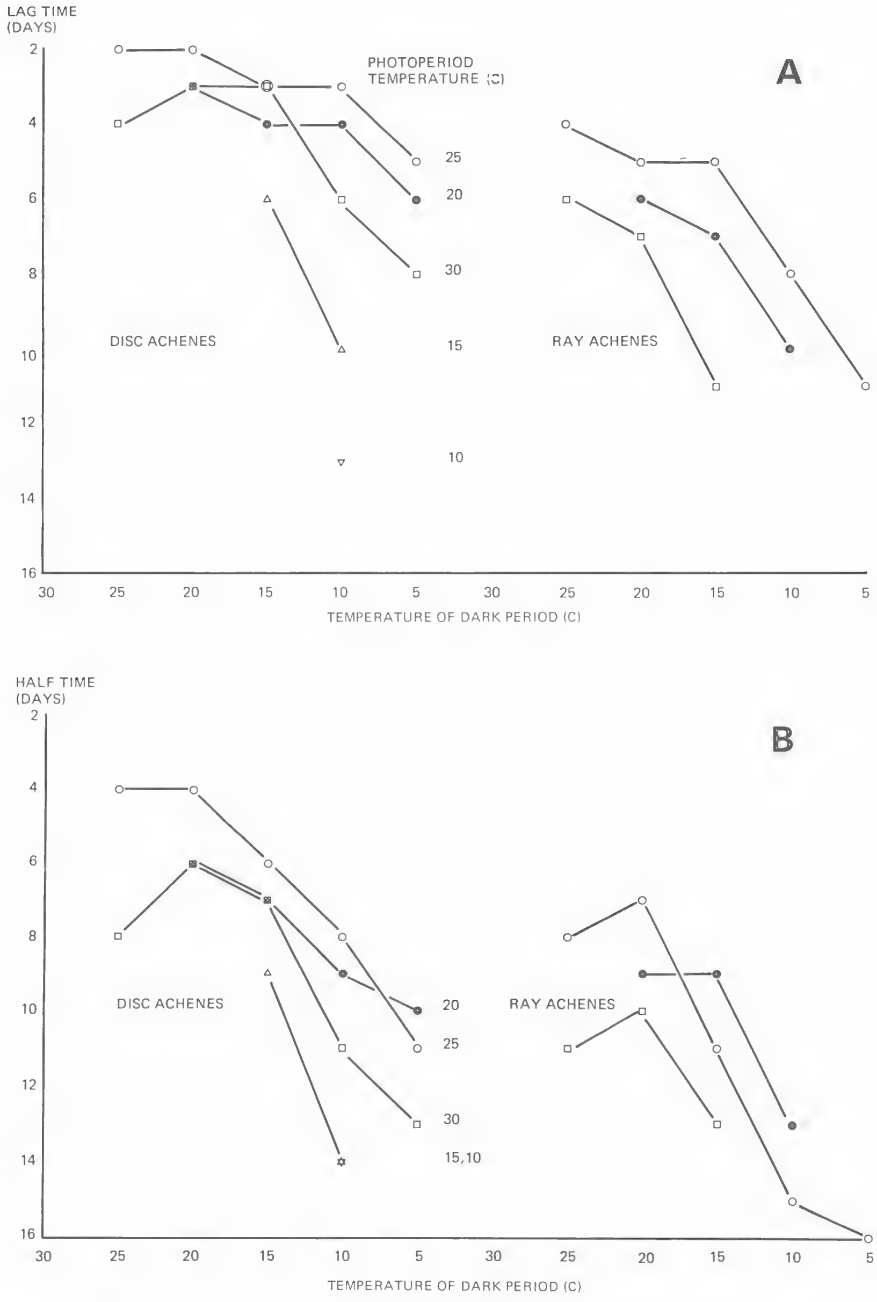


Figure 3. Rates of germination in disc and ray achenes at various temperatures with photoperiod treatment: (A) lag time, (B) halftime.

Removal of these parts in ungerminated achenes under the various temperature regimes with photoperiodic treatment resulted in from 89 to 100 percent embryo growth within 1-3 days, except at constant 5 C where 7 days were required. For embryos isolated from dark-treated achenes and returned to darkness for 10 days, the percentages were 92-98 percent. Isolated embryos from the initial dark treatments were necessarily exposed to room lights for approximately 20 min during inspection and isolation; so a possible requirement for a light stimulus for embryo growth was not excluded.

Ray achenes had perceptibly thicker pericarps, as was observed during the work with extrusion of the embryos. Mean ovendry weights of 10 sets of 10 pericarps isolated from ray achenes was 7.5 mg, significantly higher than the 5.7 mg for pericarps isolated from disc achenes. The achenes also differ consistently in length, width, and outline.

Germination after Brief Light Treatments. Compared to constant darkness, periods of illumination from 1/12 (disc achenes) or 1 h (ray achenes) to 2 x 8 h resulted in a significant increase in the germination of both types of achenes (Fig. 4). Disc achenes showed a significant increase in germination with a 1/12-h treatment and a maximum response at 1/4 h, as did ray achenes with 1/4 h and 1 h, respectively. Regular photoperiodic treatment for 30 days gave an additional 16 percent germination in disc achenes and 41 percent in ray achenes above the 2 x 8-h exposure (Fig. 4), a finding which indicates a high-intensity photoreaction or photoperiodic requirement (Koller, 1972). With their higher sensitivity to brief periods of illumination, about 35 percent of the disc achenes showed a typical phytochrome response. Approximately 10 percent of the ray achenes exhibited this response.

Germination during and after Stratification. During stratification, disc achenes germinated 9 percent and ray achenes 0 percent. Sets of ungerminated achenes transferred to 15 C/5 C with light treatments yielded 30-day percentages of 46 (disc

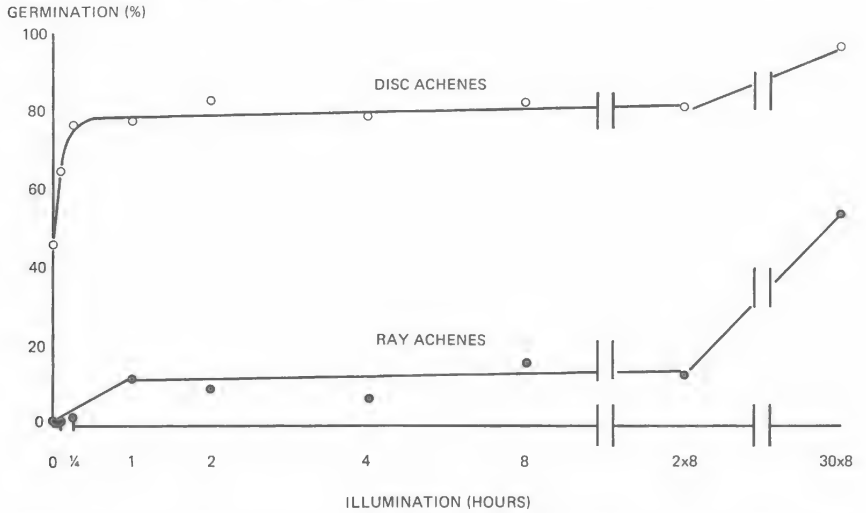


Figure 4. Thirty-day germination percentages of disc and ray achenes after short period of illumination before being returned to darkness.

achenes) and 14 (ray achenes), significantly higher than the 10 and 0 percentages for unstratified achenes. Similarly, sets transferred to 20 C/10 C in constant darkness gave 63 and 17 percent final germination for disc and ray achenes, respectively, compared to 27 and 1 percent for unstratified achenes. The 63 percent value for disc achenes included any that had germinated during stratification. Thus, low-temperature stratification had a significant effect in extending the range of temperature and light conditions for germination.

Water Relations. For imbibition periods of from 1 to 24 h, disc achenes increased in water content more rapidly and to a higher final value than did ray achenes (Fig. 5). Monitoring of the water potential of the achene-filter paper substrate showed significant differences in the changing values (Fig. 6). With 18 to 36 ray achenes per chamber, the water potentials equilibrated at –4 to –8 bars. During imbibition equivalent weights of 20-40 disc achenes, in approximately the same range of water contents, attained a temporary equilibrium in the –9 to –18 bar range early, followed by a slight-

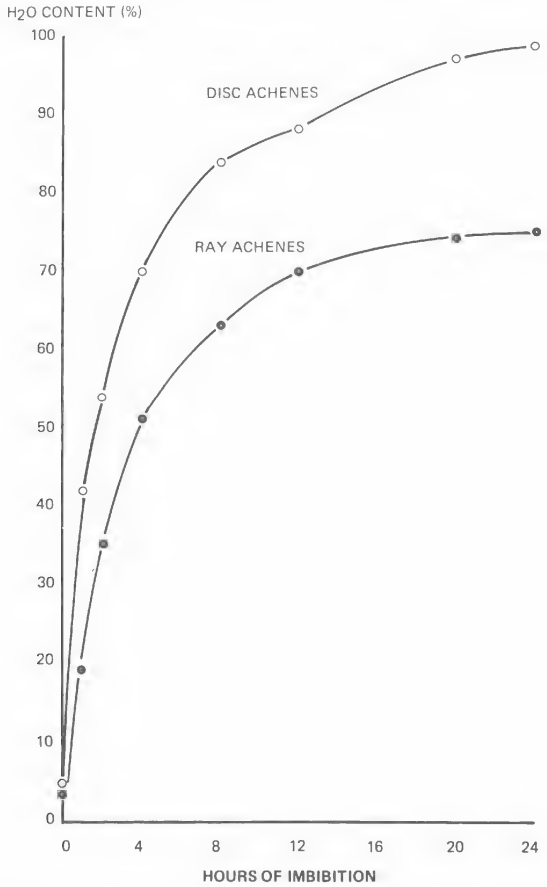


Figure 5. Water content of disc and ray achenes after varying periods of imbibition.

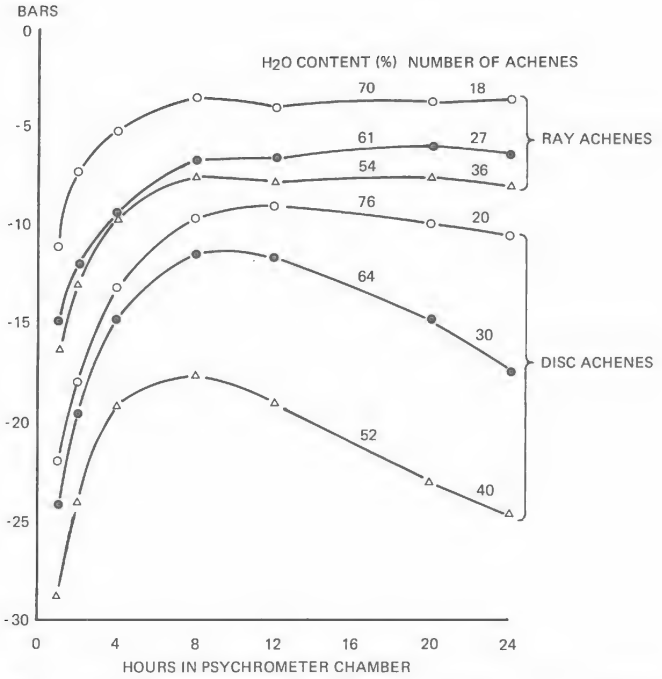


Figure 6. Water potential of disc and ray achenes during a 24-h period of imbibition in thermocouple psychrometer chambers.

to-pronounced decline to values as low as –25 bars at 52 percent water content. More generally, at water contents between 40 and 80 percent, the 24-h water potential values were uniformly lower for disc achenes at a given water content (Fig. 7).

Seedling Emergence from Soil. Under greenhouse conditions, emergence percentages for achenes on the soil surface averaged 74 and 41 percent for disc and ray achenes, respectively. Corresponding percentages for buried achenes were 19 and 0 percent. Outdoors, percentages for surface-planted and buried disc achenes were 28 and 19 percent and for ray achenes, 1 and 0 percent. Trends in emergence percentages thus followed laboratory determinations of germination percentages influenced by temperature and light, but at lower levels, presumably because of seedling mortality before emergence was detected.

Plant Development in the Greenhouse and Field. Potted plants that were continuously outdoors through the following summer bolted and completed the growth cycle; greenhouse plants remained in the rosette stage during the same period. Plants that were transferred to the coldroom for five months before being returned to the greenhouse also completed normal development during late spring and early summer. Evidently, moist stratification of the rosettes potentiates a completion of the life cycle.

Examination of the areas around five plants in late October 1971 at Tony Grove revealed 38 seedlings, four of which were identified as having derived from disc achenes and none from ray achenes. At this time, disc achenes had been completely dispersed

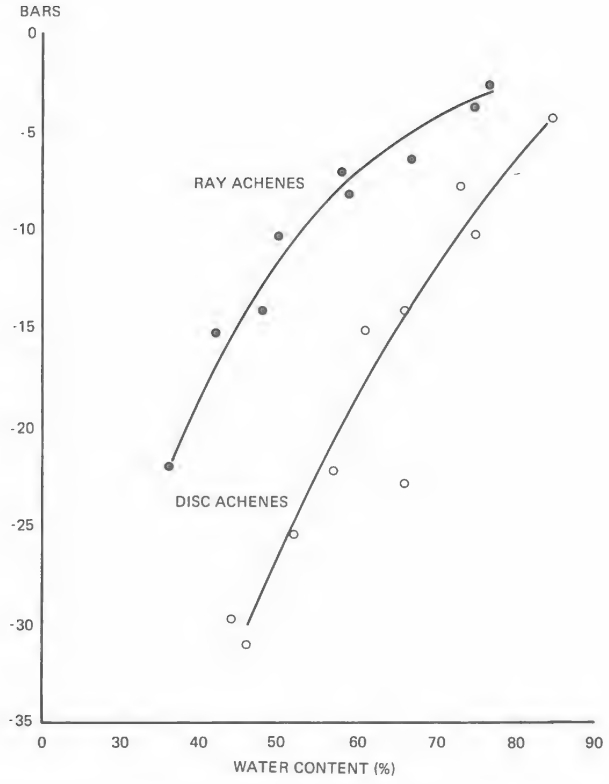


Figure 7. The 24-h water potential values of disc and ray achenes permitted to imbibe to a range of water contents. Each point represents a single determination.

from 94 of the 100 capitula examined, whereas some ray achenes were still retained in 61. All achenes had been dispersed by early June 1972, when 22 and 27 seedlings were identified from disc and ray achenes, respectively. These 49 seedlings represented about 5 percent of the approximately 900 emergent seedlings identified as gumweed. None of the 38 fall-emergent seedlings survived to mid-July. Five (one of disc acheme derivation, four from ray achenes) of the 49 spring-emergent seedlings survived the summer in the rosette stage.

Discussion

Disc achenes have less restricted optima for abundant germination (Fig. 2), attain this level over a shorter period (Fig. 3), and are less dependent upon brief and extended light stimuli for germination (Fig. 4) than are ray achenes. Differences in temperature optima and light requirements may result in different season or microsite requirements or both for appreciable germination to occur. For example, disc achenes are less light dependent; consequently, burial in soil would be tolerated at depths where temperature levels and fluctuations are less extreme than at the surface and thus more conducive to high germination. The faster germination rates of disc achenes would

allow them to take advantage of transiently favorable soil water levels, a beneficial response if seedling-root growth has kept up with a receding zone of adequate water during an ensuing dry period. Alternatively, the slower germination of ray achenes may gage adequate soil-water levels of longer duration, such as those that occur during and after snowmelt. In general, exposure to light and rapid imbibition of water by disc achenes on the soil surface soon after dissemination may create a trend toward a significant percentage of fall germination, compared to spring germination for ray achenes. Such timing affects subsequent development.

The differences in the water relations of the two types of achenes also may have significance in the responses to transient or to adequate soil-water levels of longer duration. Disc achenes attain a higher water content for a given period of imbibition (Fig. 5) and maintain a lower water potential at a given water content than do ray achenes (Fig. 6, 7). Whether these effects depend upon differences in matric forces in the pericarp or upon matric and osmotic forces in the embryo was not determined. Pregerminative processes in the more germinable disc achenes that result in increasing osmotic and matric components of the total water potential may be a factor in the decline in values during the later part of a 24-h imbibition period (Fig. 6). In any event, the effect of the lower water potential attained by disc achenes during imbibition is to maintain a more favorable gradient for water movement from the soil to the achene, an important consideration under marginal soil-water levels and one that may insure a broader range of soil-water levels for germination.

Failure of either type of achene to germinate probably results from action of the pericarp, since growth of the isolated embryo is unrestricted under the experimental conditions. The more massive pericarps of the ray achenes impose greater physical restraint. Light and low-temperature stratification treatments, reported to increase the growth potential of the embryo relative to a particular degree of mechanical restraint of the pericarp (Koller, 1972), result in improved germination. Apparently, these treatments effectively promote germination of individual achenes to the extent that they alter the balance between embryo growth and pericarp resistance to that growth. Differences in mass and possibly in chemical composition of pericarps may also have an effect on the water relations of the achenes, a consideration not determined in this study.

On high-elevation rangeland, early fall temperatures and generally dry soil would make conditions marginal for germination of disc achenes and almost entirely inhibitory for germination of ray achenes. This situation is reflected in the relatively few seedlings found on the site in October, compared to the number found after snowmelt in June. Some years, mild weather and more prolonged rains occur in October, permitting at least some germination in disc achenes and very limited germination in ray achenes. However, even under optimal conditions, not all ray achenes would be available to take advantage of them because of delayed dispersal. According to results of experiments with potted seedlings, plants that emerge in the fall overwinter and—acting as winter annuals—complete their life cycle during the next growing season. The evidence is that these plants are derived largely from disc achenes.

Abundant emergence following snowmelt probably results from a combination of factors that favorably influence germination: natural stratification, naturally eroded pericarps, optimum soil water, and rising temperatures. These spring-emergent seed-

lings remain in the rosette stage through the first growing season and complete the growth cycle the next summer. Seedlings from ray achenes probably are better represented in this crop and may constitute a majority in those years when conditions the previous fall were particularly favorable for germination and emergence of disc achenes.

In view of the beneficial effects of natural stratification of the pericarp on germination, it seems unlikley that a reserve of achenes is carried over beyond the spring. Natural erosion of the pericarp during winter with consequent weakening of its mechanical resistance to embryo growth may be another factor in promoting germination in the spring. However, a brief light stimulus may be required for growth of some embryos, particularly those of ray achenes. Deep burial may therefore represent a means of carrying over viable achenes through the second year or longer.

Literature Cited

Florez, A., and W. T. McDonough. 1974. Seed germination, and growth and development of *Rudbeckia occidentalis* Nutt. (western coneflower) on aspen range in Utah. Am. Midl. Nat. 91: 160-169.

Goldstein, A. 1974. Biostatistics. 272 p. Macmillan Co., New York.

Harper, J. L. 1965. Establishment, aggression, and cohabitation in weedy species. P. 243-268. *In*: H. G. Baker and G. L. Stebbins (eds.). The Genetics of Colonizing Species. Academic Press, New York and London.

Hitchcock, C. L., A. Cronquist, M. Ownbey, and J. W. Thompson. 1955. Vascular Plants of the Pacific Northwest, Part 5: *Compositae.* Univ. of Wash. Press, Seattle.

Koller, D. 1972. Environmental control of seed germination. P. 1-101. *In*: K. K. Kozlowski (ed.). Seed Biology, Vol. II. Academic Press, New York and London.

McDonough, W. T. 1969. Effective treatments for the induction of germination in mountain rangeland species. Northwest Sci. 43: 18-22.

———. Water potential changes in partially imbibed caryopses of *Bromus inermis* Leyss. Phyton 32(2): 107-112.

USDA Forest Service. 1937. Range Plant Handbook. U.S. Gov. Print. Off., Washington, D.C.

Received April 28, 1975.
Accepted for publication June 26, 1975.

J. W. Weber

Department of Civil and Environmental Engineering
Washington State University
Pullman, Washington 99163

Eigenvalue Analysis of an Elastostatic Sector Problem

Abtstract

Equations are derived for the stresses in a sector subjected to a prescribed loading on its circumferential edge. The radial edges are tractionless. An Airy stress function which satisfies both the governing differential equation and the boundary conditions is derived in terms of an infinite series of biharmonic (Fadle) eigenfunctions. Numerical results are presented for the 60° sector, but the method of solution is not restricted to the 60° sector and the specific circumferential loading discussed herein; the solution is applicable to an arbitrary loading on the circumferential edge of a sector of any angle. Eigenvalues for the 30°, 45°, 60°, 75°, 90°, and 120° sectors are presented, and the eigenvalue extraction method is discussed in detail in Appendix II.

Introduction

Other investigators have discussed eigenvalue extraction methods to obtain the roots of the characteristic equation (Eq. 7) discussed herein. In an early paper, Brahtz (1) discussed an eigenvalue solution in conjunction with his investigation of the stresses at the base of a gravity dam. The approximate eigenvalues he generated are given by Eqs. 10 of this paper. Horvay and Hanson (2) used a variational method to obtain approximate eigenvalues. More recently, Little and Thompson (3) used a Newton-Raphson iteration technique in the complex plane to determine the roots of Eqs. 7 of this paper. They used asymptotic expressions for the roots which were then used to obtain an initial guess for each eigenvalue.

In the analysis of the specific problem discussed herein, the author attempted to utilize the approximate eigenvalues determined by the above-mentioned authors but was unable to satisfy the boundary conditions on the radial edges of the sector when those approximate values were used. After the approximate roots (Eqs. 10) given by Brahtz were refined by the iterative method discussed in Appendix II and then used in the analysis, the author was able to satisfy the boundary conditions on the radial edges of the sector to six decimal places. The boundary conditions on these edges are quite sensitive to the accuracy of the eigenvalues. Approximate eigenvalues result in a large error in the boundary conditions on the radial edges; precisely determined roots are crucial to the analysis of the problem.

There are two requisites in the stress function method of analysis of a plane elastostatic problem: the Airy function, φ, must satisfy the governing equation, $\nabla^4\varphi = 0$, and the boundary conditions of the problem must be satisfied. The Airy function derived in this exercise meets both requirements.

Formulation of the Problem

The sector of Figure 1 has tractionless radial edges and the following loading on the circumferential boundary:

$$\left.\begin{aligned} \bar{\sigma}_r &= \frac{1}{R_o^2}\left[1-\frac{12\vartheta^2}{\gamma^2}\right] \\ \bar{\tau}_{r\vartheta} &= \frac{1}{R_o^2}\left[\vartheta-\frac{4\vartheta^3}{\gamma^2}\right] \end{aligned}\right\} \quad \text{— — — — — — — 1.)}$$

These boundary loads can be shown to represent a system in equilibrium since they can be obtained from the Airy stress function

$$\varphi_1 = -\frac{\gamma^2}{16}\left[1-\frac{4\vartheta^2}{\gamma^2}\right]^2 \quad \text{— — — — — — — — 2.)}$$

Since φ_1 does not satisfy the governing equation, $\nabla^4\varphi_1 = 0$, it cannot be used to determine the stresses at an interior point of the sector. The problem, therefore, is to determine a biharmonic function which furnishes the self-equilibrating loads (Eq. 1) on the circumferential edge and zero shear and tangential stresses on the radial boundaries.

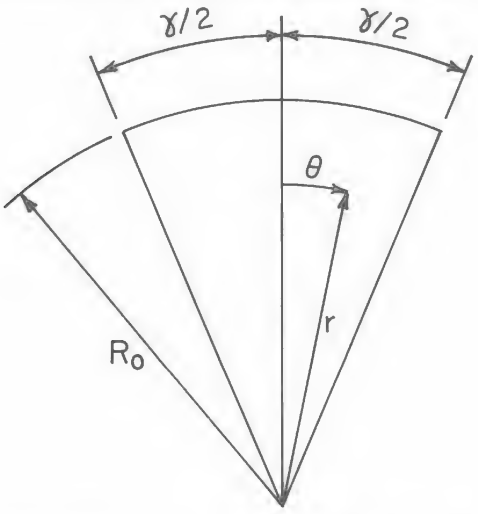


FIGURE 1. COORDINATE SYSTEM

Solution

Assume an Airy function, φ_2, represented as

$$\varphi_2 = r^{n+1}\, g(\vartheta) \quad \text{— — — — — — — — — 3.)}$$

in which n is a constant. Substitution of φ_2 into the governing differential equation, $\nabla^4\varphi_2 = 0$, yields

$$\frac{d^4g(\vartheta)}{d\vartheta^4} + 2(n^2+1)\frac{d^2g(\vartheta)}{d\vartheta^2} + (n^2-1)^2\, g(\vartheta) = 0 \quad \text{— — — — 4.)}$$

which has the solution

$$g(\vartheta) = A_1\cos(n+1)\vartheta + B_1\sin(n+1)\vartheta + C_1\cos(n-1)\vartheta + D_1\sin(n-1)\vartheta \quad \text{— — 5.)}$$

in which A_1, B_1, C_1, and D_1 are constants.

On the tractionless radial edges of the plate, the boundary conditions are

$$\left.\begin{aligned} \left[\sigma_{\vartheta_2}\right]_{\vartheta=\pm\gamma/2} &= 0 \\ \left[\tau_{r\vartheta_2}\right]_{\vartheta=\pm\gamma/2} &= 0 \end{aligned}\right\} \quad \text{— — — — — — — 6a.)}$$

Since $\sigma_{\vartheta_2} = \dfrac{\partial^2 \vartheta_2}{\partial r^2}$ and $\tau_{r\vartheta_2} = -\dfrac{\partial}{\partial r}\left[\dfrac{1}{r}\dfrac{\partial \varphi_2}{\partial \vartheta}\right]$, the preceding boundary conditions become

$$\left.\begin{aligned} \left|g(\vartheta)\right|_{\vartheta=\pm\gamma/2} &= 0 \\ \left|\frac{dg(\vartheta)}{d(\vartheta)}\right|_{\vartheta=\pm\gamma/2} &= 0 \end{aligned}\right\} \quad \text{— — — — — — — 6b.)}$$

Two equations result when $g(\vartheta)$ from Eq. 5 is substituted into Eqs. 6b:

$$A_1 \cos(n+1)\frac{\gamma}{2} + C_1 \cos(n-1)\frac{\gamma}{2} = 0$$

$$A_1(n+1) \sin(n+1)\frac{\gamma}{2} + C_1(n-1) \sin(n-1)\frac{\gamma}{2} = 0$$

To ensure that A_1 and C_1 both do not equal zero, the determinant of the coefficients of A_1 and C_1 in the preceding equations must vanish; therefore,

$$\begin{vmatrix} \cos(n+1)\dfrac{\gamma}{2} & \cos(n-1)\dfrac{\gamma}{2} \\ (n+1) \sin(n+1)\dfrac{\gamma}{2} & (n-1) \sin(n-1)\dfrac{\gamma}{2} \end{vmatrix} = 0$$

The preceding determinant reduces to the characteristic equation

$$n \sin\gamma = -\sin n\gamma \quad \text{— — — — — — — — — 7.)}$$

In the interval $0° \leq \gamma \leq 180°$, the only real roots of Eq. 7 occur when $\gamma = 180°$ and are equal to $n = 1.00, 2.00, 3.00, \cdots$. The roots for all other γ in this range are complex and can be represented as

$$n = a_n + ib_n \quad \text{— — — — — — — — — 8.)}$$

Substitution of Eq. 8 into Eq. 7 yields two equations, one from the imaginary terms and the other from the real terms. The equations are

$$\left.\begin{aligned} \sin a_n\gamma \cosh b_n\gamma &= \pm a_n \sin\gamma \\ \cos a_n\gamma \sinh b_n\gamma &= \pm b_n \sin\gamma \end{aligned}\right\} \quad \text{— — — — — — 9.)}$$

Eigenvalues (a_n and b_n) for the symmetric problem are associated with the negative

sign on the right side of Eq. 9; the positive sign is for the case of an antisymmetric problem.

Brahtz developed the following equations for determining approximate eigenvalues:

$$\left.\begin{aligned} a_k &= \frac{\pi(2k+1) - \varepsilon_k}{\gamma^2} \\ b_k &= \frac{1}{\gamma}\log_e\left\{\left[\frac{\pi(2k+1) - \varepsilon_k}{\gamma}\right]\sin\gamma\right\} \end{aligned}\right\} \quad \text{— — — — — — 10.)}$$

in which

$$\varepsilon_k = \frac{4\ \log_e\left[\dfrac{\pi(2k+1)\ \sin\gamma}{\gamma}\right]}{\pi(2k+1)}$$

and

$$k = 1,\ 2,\ 3,\ \cdots .$$

Manipulation of Eq. 9 yields

$$b_n\ \sin\gamma = \frac{\cos\ a_n\gamma}{\sin\ a_n\gamma}\left[a_n{}^2\ \sin^2\gamma - \sin^2\ a_n\gamma\right]^{1/2} \quad \text{— — — — — 11.)}$$

By the iterative technique employed in the solution of Eqs. 11, the approximate values, a_k, rounded off to the nearest tenth's decimal place, are substituted into Eq. 11 for a_n. The tenth's decimal place of a_n is varied from 0 to 9, and each value of a_n generates a corresponding value of b_n by Eq. 11. That pair of a_n and b_n which best satisfies Eq. 11 is selected; a_n is substituted back into Eq. 11, and the procedure is repeated by varying the hundredth's decimal place of the previously refined value of a_n. Each successive iteration refines a_n and b_n to one more decimal place. The iterative procedure, in its entirety, is presented in Appendix II.

Since each sectorial angle, γ, has an infinite number of n's satisfying Eq. 7, the Airy function, φ_2, of Eq. 3 can be written as

$$\varphi = \sum_{n=1}^{\infty} K_n\ r^{n+1}\left[\cos(n-1)\frac{\gamma}{2}\cos(n+1)\vartheta - \cos(n+1)\frac{\gamma}{2}\cos(n-1)\vartheta\right] \quad \text{— — 12.)}$$

in which

$$K_n = \frac{-C_1}{\cos(n+1)\dfrac{\gamma}{2}}$$

By the theory of elasticity, the known expressions for stress in terms of an Airy function are

$$\sigma_{r_2} = \frac{1}{r}\left[\frac{\partial\,\varphi_2}{\partial\ r}\right] + \frac{1}{r^2}\left[\frac{\partial^2\varphi_2}{\partial\,\vartheta^2}\right]$$

$$\sigma_{\vartheta_2} = \frac{\partial^2 \varphi_2}{\partial r^2}$$

$$\tau_{r\vartheta_2} = -\frac{\partial}{\partial r}\left[\frac{1}{r}\frac{\partial \vartheta_2}{\partial \vartheta}\right]$$

Since Eq. 12 is complex, differentiation of φ_2 in accordance with the preceding equations yields both real and imaginary components for the stresses. Only the real components are used, and they are

$$\left.\begin{aligned}
R_o^2\sigma_{r_2} &= \sum_{n=1}^{\infty} \rho\, a_n{}^{-1}\left[K_{1n}(M'\Psi_{1n} - N'\Psi_{2n}) - K_{2n}(N'\Psi_{1n} + M'\Psi_{2n})\right] \\
R_o^2\tau_{r\vartheta_2} &= -\sum_{n=1}^{\infty} \rho\, a_n{}^{-1}\left[K_{1n}(M'\Gamma_{1n} - N'\Gamma_{2n}) - K_{2n}(N'\Gamma_{1n} + M'\Gamma_{2n})\right] \\
R_o^2\sigma_{\vartheta_2} &= \sum_{n=1}^{\infty} \rho\, a_n{}^{-1}\left[K_{1n}(M'X_{1n} - N'X_{2n}) - K_{2n}(N'X_{1n} + M'X_{2n})\right]
\end{aligned}\right\} \text{---------- 13.)}$$

Eqs. 13 determine the stresses at any point in the sector. The unknowns in the preceding equations are K_{1n} and K_{2n}; the remaining quantities are all functions of a_n and b_n and are known as biharmonic eigenfunctions. In Eqs. 13, the following expressions are used: $\rho = r/R_o$; $M' = \cos(\text{bln}\ \rho)$; $N' = \sin(\text{bln}\ \rho)$; and

$$\begin{aligned}
\Psi_{1n} &= TA_n - UB_n + PE_n - QF_n \\
\Psi_{2n} &= -UA_n - TB_n + QE_n + PF_n \\
\Gamma_{1n} &= -VG_n + WH_n + RJ_n - SL_n
\end{aligned}
\qquad
\begin{aligned}
\Gamma_{2n} &= -VH_n - WG_n + RL_n + SJ_n \\
X_{1n} &= -TA_n + UB_n - PC_n + QD_n \\
X_{2n} &= TB_n + UA_n - PD_n - QC_n
\end{aligned}$$

in which

$$\begin{aligned}
A_n &= F_n{}^*Q_1 - E_n{}^*P_1 \\
B_n &= E_n{}^*Q_1 + F_n{}^*P_1 \\
C_n &= E_n{}^*T_1 + F_n{}^*U_1 \\
D_n &= F_n{}^*T_1 - E_n{}^*U_1 \\
E_n &= G_n{}^*T_1 + H_n{}^*U_1
\end{aligned}
\qquad
\begin{aligned}
F_n &= H_n{}^*T_1 - G_n{}^*U_1 \\
R &= \sin(a_n - 1)\vartheta\ \cosh\ b_n\vartheta \\
S &= \cos(a_n - 1)\vartheta\ \sinh\ b_n\vartheta \\
V &= \sin(a_n + 1)\vartheta\ \cosh\ b_n\vartheta \\
W &= \cos(a_n + 1)\vartheta\ \sinh\ b_n\vartheta
\end{aligned}$$

and

$$\begin{aligned}
E_n{}^* &= a_n^2 - b_n^2 + a_n \\
F_n{}^* &= b_n + 2a_nb_n \\
G_n{}^* &= a_n^2 - b_n^2 - 3a_n
\end{aligned}
\qquad
\begin{aligned}
H_n{}^* &= 2a_nb_n - 3b_n \\
J_n{}^* &= a_n^2 - b_n^2 - a_n \\
L_n{}^* &= 2a_nb_n - b_n
\end{aligned}$$

The unknowns K_{1n} and K_{2n} in Eqs. 13 can be determined from the following boundary conditions on the circumferential edge of the plate:

$$\left.\begin{aligned}
\left[\sigma_{r_2}\right]_{r=R} &= \bar{\sigma}_r \\
\left[\tau_{r\vartheta_2}\right]_{r=R} &= \bar{\tau}_{r\vartheta}
\end{aligned}\right\} \text{---------- 14a.)}$$

By Eqs. 1 and 13, the preceding boundary conditions become

$$\left.\begin{aligned}
\sum_{n=1}^{\infty} (K_{1n}\Psi_{1n} - K_{2n}\Psi_{2n}) &= 1 - \frac{12\vartheta^2}{\gamma^2} \\
\sum_{n=1}^{\infty} (K_{1n}\Gamma_{1n} - K_{2n}\Gamma_{2n}) &= \vartheta - \frac{4\vartheta^3}{\gamma^2}
\end{aligned}\right\} \text{---------- 14b.)}$$

K_{1n} and K_{2n} were determined by the method of collocations. Five collocation points require five pairs of eigenvalues, and the expansion of Eqs. 14b with five pairs of eigenvalues yields ten equations in terms of ten unknown constants: K_{11}, K_{12}, K_{13}, K_{14}, K_{15}, K_{21}, K_{22}, K_{23}, K_{24}, and K_{25}. A numerical solution was generated for the 60° sector utilizing the eigenvalues of Table 1.

TABLE 1. Eigenvalues for the equations $\sin a_n\gamma\cosh b_n\gamma = -a_n\sin\gamma$, $\cos a_n\gamma\sinh b_n\gamma = -b_n\sin\gamma$.

$\gamma =$ 30°	a_1	a_3	a_5	a_7	a_9
	8.06296510	20.46721420	32.61272710	44.69125580	56.74125140
	b_1	b_3	b_5	b_7	b_9
	4.20286721	5.83660141	6.69310361	7.28117457	7.72996777
$\gamma =$ 45°	a_1	a_3	a_5	a_7	a_9
	5.39052940	13.65142760	21.74607660	29.79731160	37.82998910
	b_1	b_3	b_5	b_7	b_9
	2.72040954	3.81446502	4.38632240	4.77858034	5.07802655
$\gamma =$ 60°	a_1	a_3	a_5	a_7	a_9
	4.05932900	10.24572693	16.31416346	22.35138131	28.37518334
	b_1	b_3	b_5	b_7	b_9
	1.95204969	2.77796301	3.20778899	3.50239786	3.72707165
$\gamma =$ 75°	a_1	a_3	a_5	a_7	a_9
	3.26501250	8.20425240	13.05627122	17.88475030	22.70303473
	b_1	b_3	b_5	b_7	b_9
	1.46666459	2.13337291	2.47825705	2.71431532	2.89423319
$\gamma =$ 90°	a_1	a_3	a_5	a_7	a_9
	2.73959330	6.84513506	10.88555219	14.90789058	18.92231171
	b_1	b_3	b_5	b_7	b_9
	1.11902459	1.68163464	1.97019946	2.16733263	2.31746456
$\gamma =$ 120°	a_1	a_3	a_5	a_7	a_9
	2.09413908	5.15173009	8.17576424	11.18950207	14.19854503
	b_1	b_3	b_5	b_7	b_9
	0.60458498	1.04933008	1.26896453	1.41792756	1.53105086

TABLE 2. Stresses along circumferential boundary of the 60° sector (starred values indicate collocation points).

ϑ	$\bar{\sigma}_r$	σ_{r_2}	$\bar{\tau}_{r\vartheta}$	$\tau_{r\vartheta_2}$
0°	1.000000	1.013840	0.000000	0.000000
*5°	0.916668	0.916659	0.084884	0.084838
*10°	0.666666	0.666674	0.155140	0.155150
*15°	0.250002	0.250001	0.196349	0.196334
*20°	–0.333334	–0.333344	0.193925	0.193937
*25°	–1.083330	–1.083317	0.133324	0.133324
30°	–2.000020	–2.055078	0.000000	0.000001

The Airy function, φ_2, was derived to reproduce the given tractions on the circumferential boundary. The values in Table 2 indicate that φ_2 reproduced the stresses along this edge of the sector within four decimal places of their true values. Table 3 indicates how well the stresses are reproduced between points of collocation. Using a truncated series with five pairs of eigenvalues (alternate pairs beginning with a_1 and b_1) and the equations for σ_{r_2} and $\tau_{r\vartheta_2}$ of Eqs. 13 in Eqs. 6a, the boundary conditions on the radial edges are satisfied to six decimal places.

Conclusions

A method for determining the Airy stress function for a sector with tractionless radial edges and a self-equilibrating loading on the circumferential boundary is presented as a series of biharmonic eigenfunctions. Since the Airy stress function satisfies both the governing elasticity equation ($\nabla^4\varphi = 0$) and the boundary conditions on the radial edges of the sector, the method of solution is applicable to a sector of any angle with an arbitrary, self-equilibrating load on the circumferential boundary. The eigenvalues

TABLE 3. Stresses at points of noncollocation along the circumferential boundary of the 60° sector.

ϑ	$\bar{\sigma}_r$	σ_{r_2}	$\bar{\tau}_{r\vartheta}$	$\tau_{r\vartheta_2}$
3°	0.9700	0.9750	0.0518	0.0514
8°	0.7866	0.7850	0.1297	0.1307
13°	0.4366	0.4370	0.1842	0.1834
18°	−0.0800	−0.0816	0.2010	0.2022
23°	−0.7633	−0.7637	0.1654	0.1659

Appendix I—Notation

a_n = eigenvalue representing the real part of n;
b_n = eigenvalue representing the imaginary part of n;
i = imaginary unit;
n = $a_n + ib_n$, root of characteristic equation;
R_o = radius of sector;
r = radial coordinate;
γ = sector angle;
ϑ = angular coordinate;
ρ = r/R_o, dimensionless radial coordinate;
σ_ϑ = tangential stress;
σ_ρ = radial stress;
$\tau_{r\vartheta}$ = shear stress;
φ = Airy stress function.

in Table 1 apply to any symmetric sector problem involving tractionless radial edges. The iterative technique discussed in Appendix II can be used to determine the roots of Eqs. 9 for a sector of any angle, γ.

Appendix II—Eigenvalue Determination

The following FORTRAN program generates 12 pairs of eigenvalues, a_n and b_n, for $\gamma = 90°$. Eigenvalues for other sectors are determined by making the appropriate changes in the arguments of the trigonometric functions appearing in the program. Twelve approximate values of a_k from Eqs. 10, all rounded off to the nearest tenth's decimal place, are entered into the program under A(I). To obtain all of the eigen-

values, a second run of the program usually is necessary. In the second run, values of a_k rounded off to the nearest hundredth's decimal place are entered into the program, requiring the modification of AA(M,N). The modified expression becomes AA(M,N) =A(N)-(.1D0-.01D0*(XM-1.D0))/10.D0**I . The following notation is used: S=sinγ; SA=sin$a_n\gamma$; CA=cos$a_n\gamma$; X=$a_n^2\sin^2\gamma$-$\sin^2 a_n\gamma$; Y=$\sqrt{X}$.

```
      DIMENSION A(12),B(12),R(12),AA(21,12),AB(21,12),BB(21,12),ER(21)
      READ (5,20)  (A(I), I=1,12)
   20 FORMAT (11F 7.2/F 7.2)
      PI = 3.14159265
      DO 100 N=1,12
      DO 100 I=1,6
      DO 50  M=1,21
      XM=M
      AA(M,N)= A(N)- (1.DO-.1DO*XM)/10.DO**I
      S= DSIN(PI/2.DO)
      CA= DCOS(AA(M,N)*PI/2.DO)
      SA= DSIN(AA(M,N)*PI/2.DO)
      X= AA(M,N)**2*S**2-SA*SA
      Y= DSQRT(X)
      BB(M,N)=CA*Y/(SA*S)
      HCB= DCOSH(BB(M,N)* PI/2.DO)
      AB(M,N)= DABS(SA*HCB/S)
   50 ER (M)= DABS(AA(M,N)-AB(M,N))
      DO 100  M=1,20
      R(N) = ER(M)-ER(M+1)
      IF  (R(N)) 100,100, 40
   40 R(N)=ER(M+1)
      A(N)=AA(M+1,N)
      B(N)=BB(M+1,N)
  100 CONTINUE
      WRITE (6,30) (A(I), B(I), R(I), I=1,12)
   30 FORMAT (3F 20.8)
      STOP
      END
```

References

1. Brahtz, J. H. A., "The Stress Function and Photoelasticity Applied to Dams," Transactions of the American Society of Civil Engineers, Vol. 101, 1936, pp. 1240-1277.
2. Horvay, G., and Hanson, K. L., "The Sector Problem," *Journal of Applied Mechanics,* Transactions of the American Society of Mechanical Engineers, Vol. 24, 1957, pp. 574-581.
3. Little, R. W., and Thompson, T. R., "End Effects in Truncated Semi-Infinite Wedge," *Journal of the Engineering Mechanics Division,* Proceedings of the American Society of Civil Engineers, Vol. 98, No. EM5, October, 1972, pp. 1239-1251.

Received May 12, 1975.
Accepted for publication July 7, 1975.

Henry W. Smith
Rose Okazaki

Department of Agronomy and Soils
Washington State University
Pullman, Washington 99163

and

Charles R. Knowles

Idaho Bureau of Mines and Geology
Moscow, Idaho 83843

Electron Microprobe Analysis as a Test of the Correlation of West Blacktail Ash with Mount St. Helens Pyroclastic Layer T[1]

Abstract

Scanning electron micrographs illustrate the morphology of vesicular glass shards from the West Blacktail ash. These contrast sharply with shards having tubular voids. Electron microprobe analysis of the glass for content of Ca, K, and Fe shows no difference between this ash and Mount St. Helens pyroclastic layer T. The correlation of the two tephra layers is supported.

Many soils of northern Idaho and adjacent northeastern Washington, plus some in northwestern Montana, have a discrete near-surface layer of sediment, the West Blacktail ash (Smith, Okazaki, and Aarstad, 1968). We have considered it a single widespread depositional layer because of several constant properties. These include (1) dominance of coarse vesicular forms among the glass shards, (2) a constant suite of phenocrysts, and (3) a refractive index of glass shards between 1.497 and 1.501. Such nonconstant features as content of fine sand and extent of dominance of hypersthene among the phenocrysts we attributed to aerial differentiation as the dust moved over the region. Later (Okazaki *et al.,* 1972), we correlated the West Blacktail ash with layer T, a product of Mount St. Helens (Crandell *et al.,* 1962; Mullineaux, 1964). We based this correlation chiefly upon similarities of data for (1) age, (2) phenocryst suite, and (3) morphology plus optical properties of glass shards and certain phenocrysts. We did not demonstrate complete geographic continuity.

In this paper we present additional information for testing the correlation of the two tephra layers; this consists of scanning electron micrographs of glass shards, and the content of Ca, K, and Fe in these shards. "Tephra" applies to all airborne debris from a volcanic vent, with no size limits implied. Thorarinsson, who proposed the word, has reviewed its origin and usage (Westgate and Gold, 1974).

Morphology of Glass Shards

During our first microscopic examination of samples of West Blacktail ash, in 1962, we were chiefly impressed by the dominance of shards with subspherical vesicles and fragile vesicle walls; platy fragments and shards with tubular voids were sparse.

[1] Scientific Paper No. SP4407. College of Agriculture, Research Center, Washington State University, Pullman, Washington 99163, Project 0193.

Vesicular glass occurred as discrete grains, but it also encased crystals of several minerals in the sand and silt separates. The morphology of these glass shards was in definite contrast to that characterizing samples attributed to Mount Mazama, in which the dominant forms have gently curved tubular voids, and the separating glass is thicker.

These two forms, tubular and vesicular, as viewed under a petrographic microscope, are shown in Figure 1, A and B. One must imagine the three-dimensional details, because of the narrow depth of field. But details do become evident under the scanning electron microscope (Fig. 1, C through F). Such views lend support to the morphological distinctions that were vital when we were determining the area of major fallout of the West Blacktail ash, since field identification was less certain as we approached the geographic margins. The usefulness of glass morphology was equally great as we checked presumed distinctions between the West Blacktail ash and the tephra grains in the underlying soil horizons.

Visitors in our laboratory have at times expressed the view that vesicular shards might in fact be aggregates of volcanic dust (accretionary lapilli). As viewed with transmitted light and with a negligible depth of field, particularly when one's view is obscured by surface weathering products, the particle might indeed appear to have such an origin. However, the details of each bubble wall that are visible under the scanning electron microscope, after being seen repeatedly in shards such as those illustrated in Figure 1, favor another explanation—a solidified bit of froth.

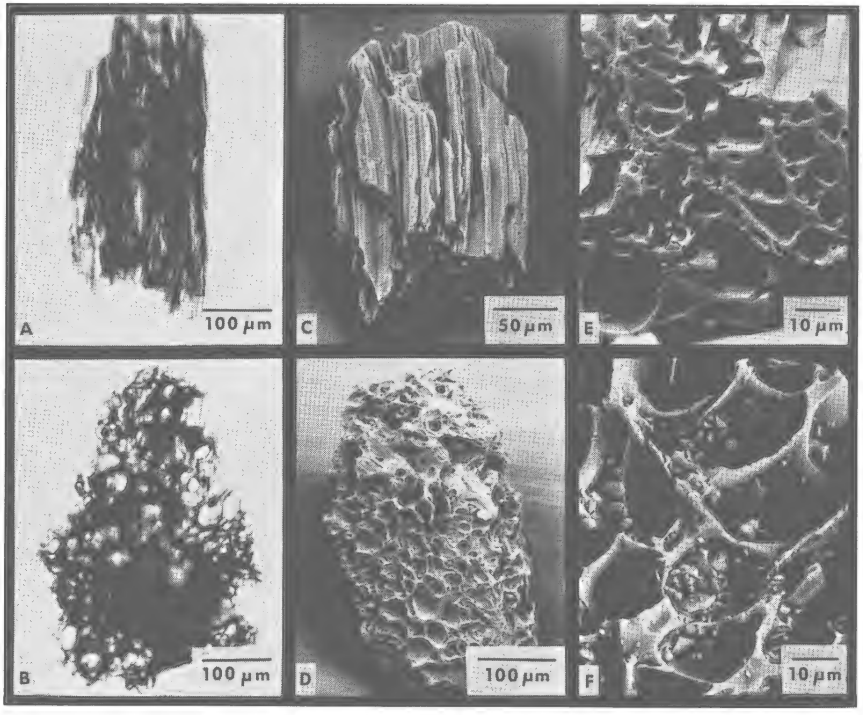


Figure 1. Photomicrographs (A and B) and scanning electron micrographs (C through F) of glass shards with tubular voids (A, C, and E) and subspherical voids (B, D, and F).

Another conclusion, not related to tephra identification, but rather to the procedure of particle-size analysis as applied to tephra-containing samples, is inescapable. This is the futility of attempting to obtain meaningful numbers for content of silt and clay, if many of the grains are glass shards with fragile bubble walls, and if many bubble cavities are partially filled with debris (Fig. 1, D and F). This error source is in addition to the better known one of a modified particle-settling rate because of stable voids (Fig. 1, C and E).

Elemental Analysis of Glass Shards

Following the appearance of stimulating reports by Wilcox and Powers (Wilcox and Powers, 1964; Powers and Wilcox, 1964; Wilcox, 1965), numerous parameters for tephra characterization were developed. Most of that research turned from optical properties to chemical analyses (e.g., Borchardt, Harward, and Schmitt, 1971; Randle, Goles, and Kittleman, 1971; Dudas, Harward, and Schmitt, 1973). Any bulk-sample approach has two inherent weaknesses: (1) imperfect segregation of tephra components of unlike chemical compositions, and (2) analysis of weathered surfaces along with the less-altered interiors of grains. The seriousness of these problems is variable, depending upon the technique of sample preparation, and upon the content of microlites. However, analysis with electron microprobe equipment should reduce these problems to a minimum, since the volumes analyzed are interior portions of grains, exposed by polishing, and each is examined individually, both optically and chemically. Selection on the polished surface of the sample allows for omission of included foreign matter and minimizes oxidized surface effects.

Smith, Westgate, and Tomlinson, at the University of Alberta, have developed and tested microprobe procedures for analyzing tephra (Smith and Westgate, 1969; Smith, Westgate, and Tomlinson, 1969; Westgate, Smith, and Tomlinson, 1970). They settled upon a procedure with these steps: (1) concentrate the component to be analyzed; (2) mount the grains in epoxy resin; (3) grind and polish the mounts to expose component interiors; (4) coat the grain surfaces with a carbon film; (5) select suitable surfaces for analysis; (6) record counts from 50 shards for 20 seconds each; (7) compare the data with counts from analyzed standards; and (8) calculate content of the elements selected.

Our procedure departed somewhat from that used at the University of Alberta. We handpicked glass shards, instead of using flotation methods, in order to have few phenocrysts to avoid during the analysis. The number of shards as well as the number of separate volumes analyzed per shard were not constant, but varied depending upon the uniformity of the accumulating data during each run. For the usual sample we analyzed 20 separate volumes, using a counting time of 10 seconds. Smith and Westgate (1969) recommended positioning the electron beam on ". . . the rib-like glass of the pumice or the characteristic thin curved cross sections of typical shards." This procedure is readily accomplished with samples like those attributed to Mount Mazama, in which the dominant shards have tubular voids, and the cross-section of the separating glass accommodates the electron beam (*ca.* $1\mu m^2$). Selecting a suitable polished surface is more difficult when the walls separating subspherical vesicles are extremely thin (Fig. 1). We recorded data for Ca, Mg, Al, Fe, and K, but report only those for Ca, K, and Fe. These three elements were previously found useful for characterizing the glass component of similar tephra (Westgate, Smith, and Tomlinson, 1970).

Analytical Data

The ordering of samples in Table 1 is by airline distance from Mount St. Helens, extending from the base of the volcano to 190 km. for tephra T, and ranging from 350 to 610 km. for the West Blacktail ash. Data for content of Ca, K, and Fe show no trend in relation to distance from the presumed source.

Variation among data within each of the two sets of samples (Table 1) is greater for Fe than for Ca or K. Hand specimens of pumice from tephra T are characteristically easy to break along irregular weathering planes, which are stained with iron-bearing weathering products. If this internal alteration persists on a microscale, some of the surfaces exposed for analysis during the polishing of epoxy mounts would not be solely unaltered glass, as is hoped. This circumstance may be the reason for part of the variation in iron content. The percentage of Ca exceeds that of K except in one sample of each set. The Ca:K:Fe proportions are about 1.0:0.9:1.2 for both the West Blacktail and the layer T samples.

The elemental data in Table 1 are plotted in Figure 2. Either a ternary diagram or a plotting of the content of one element against the ratio of the other two would be suitable. The ternary presentation follows the convention of Westgate, Smith, and

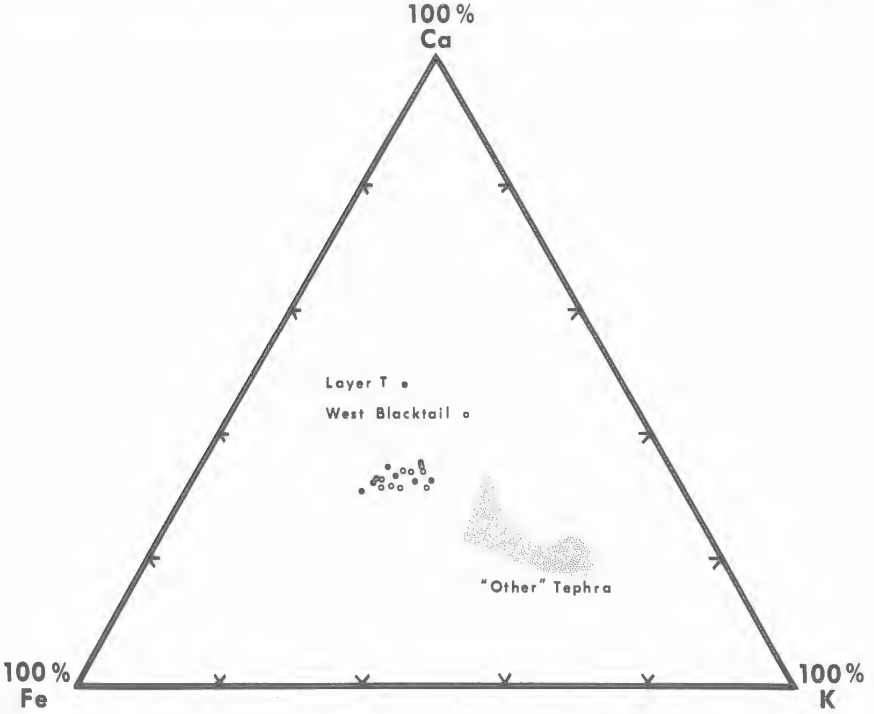


Figure 2. Electron microprobe data for Ca, K, and Fe (sum = 100%) in glass shards from samples assigned to West Blacktail ash and pyroclastic layer T. The outlined area encompasses all available analogous data for "other" tephra: those of all ages known to occur within or near the area of fallout of the West Blacktail ash. These are Glacier Peak (upper and lower), Mount Mazama, Mount St. Helens W and Y, Bridge River (three types), and a tephra of unknown origin that is common north of Wenatchee, both east and west of the Okanogan River.

TABLE 1. Calcium, potassium, and iron content of glass shards.[1]

Sample No.	Identification	Location		Weight % of Ca	K	Fe	Proportion of Ca	:	K	:	Fe
			Samples previously assigned to Mount St. Helens tephra T								
1	Timberline	26- 9N- 5EWM, WA		1.69	1.63	1.93	1.00	:	0.96	:	1.14
2	Lawrence	22- 9N- 5EWM, WA		1.98	1.55	2.50	1.00	:	0.78	:	1.26
3	Iron Creek	31-10N- 7EWM, WA		1.78	1.84	1.91	1.00	:	1.03	:	1.07
4	Smith Creek	5-11N- 9EWM, WA		2.01	1.51	2.26	1.00	:	0.75	:	1.12
5	Road 1415	2-13N-11EWM, WA		1.81	1.47	2.67	1.00	:	0.81	:	1.48
6	Granite Lake	9-15N-12EWM, WA		1.80	1.54	2.11	1.00	:	0.86	:	1.17
7	Table Mountain	27-20N-18EWM, WA		2.13	1.85	2.06	1.00	:	0.87	:	0.97
8	Colockum Pass	25-20N-20EWM, WA		1.98	1.58	2.61	1.00	:	0.80	:	1.32
			Mean	1.90	1.62	2.26	1.00	:	0.86	:	1.19
			S.D.	0.15	0.15	0.30					
			Samples previously assigned to West Blacktail ash								
9	Creston Bog	13-26N-34EWM, WA		1.90	1.53	2.39	1.00	:	0.81	:	1.26
10	Usk-26	28-33N-44EWM, WA		1.78	1.53	2.39	1.00	:	0.86	:	1.34
11	Squaw Creek-37	19-35N-41EWM, WA		1.88	1.68	1.85	1.00	:	0.89	:	0.98
12	Pass Ck. Pass-1	12-38N-44EWM, WA		1.70	1.60	1.73	1.00	:	0.94	:	1.02
13	Pass Ck. Pass-2	17-38N-45EWM, WA		1.74	1.67	2.19	1.00	:	0.96	:	1.26
14	West Blacktail	27-62N- 5WBM, ID		1.76	1.59	2.27	1.00	:	0.90	:	1.29
15	Hager Lake	34-61N- 5WBM, ID		1.84	1.64	1.99	1.00	:	0.89	:	1.08
16	Black Mountain	29-61N- 2 EBM, ID		1.89	1.61	2.08	1.00	:	0.85	:	1.10
17	Northwest Peak	20-65N-33WPM, MT		1.63	1.75	1.87	1.00	:	1.07	:	1.15
			Mean	1.79	1.62	2.08	1.00	:	0.91	:	1.16
			S.D.	0.09	0.07	0.24					

[1]The data were collected on an ARL-EMX microprobe at the Idaho Bureau of Mines and Geology. The data are relative to a University of Alberta obsidian standard described by Smith and Westgate (1969).

Tomlinson (1970). (In a personal communication, D. G. W. Smith notes that the captions and labels in their Table 2 and Figures 1, 2, and 3 should indicate oxides, rather than elements.) For these diagrams the sum of the weight percentages of Ca, K, and Fe is set equal to 100%. The area covered by the cluster of data points is a measure of variability among the samples. Within the cluster of symbols those for the West Blacktail ash and pyroclastic layer T samples are intermixed; i.e., the two tephra layers are not separable by this parameter. The acceptability of the earlier correlation of the two, based on other parameters, is enhanced.

Unequivocal identification of a tephra sample is not likely. That would require both certain knowledge of all tephra layers in the sampling area, and the existence of unique, known, and measurable properties for each. In northeastern Washington these requirements have not been met.

Many but not all of the known tephra layers have been documented by stratigraphic and optical means, and some have been characterized by chemical data. In Figure 2 only an area is shown for "other" tephra samples. Within that area would be all of the symbols representing Ca-K-Fe microprobe data available to us, for tephra samples that were collected within or near the area of occurrence of the West Blacktail ash. Some of these tephra layers, e.g., Glacier Peak and Mazama, are so different by other parameters as to make any confusion unlikely. Attribution includes Glacier Peak, Mount Mazama, Mount St. Helens W and Y, Bridge River, and samples not identified by source but plotted as to sampling location by Okazaki et al. (1972). These samples, now under study, were collected south of Lake Chelan and in the Okanogan Highlands. In the 1972 paper, page 80, they are located by a "+" symbol. Sources of the data are Smith and Westgate (1969); Westgate, Smith, and Tomlinson (1970); and unpublished work by the writers. The area shown in Figure 2 for data from these samples is well-separated from the cluster of data points for samples attributed to pyroclastic layer T and West Blacktail ash.

Microprobe data for Ca, K, and Fe in glass shards, then, can be added to previously used properties for separating these two tephra layers from several others known to occur within or near the same area.

Summary

In other publications we presented field and petrographic data for the characterization and correlation of two tephra layers. These are the West Blacktail ash and pyroclastic layer T from the 1800 A.D. eruption of Mount St. Helens. Since we did not demonstrate geographic continuity for the two layers, we wished to test our correlation using another parameter. We chose partial elemental analysis of glass shards selected from eight samples assigned to West Blacktail ash and from nine samples assigned to pyroclastic layer T. Analysis was by an electron microprobe technique, essentially that developed at the University of Alberta by Smith, Westgate, and Tomlinson. Since they had already determined which elements were diagnostic for the identification and correlation of similar tephra, no background research was needed. Proportions among Ca, K, and Fe for each tephra are 1.0:0.9:1.2. The correlation of the two layers is supported by these chemical data. Other tephra layers occur within or near the area of fallout for West Blacktail ash. Among the useful parameters for distinguishing them are the lower Ca/K ratios in the glass shards.

Acknowledgements

We thank Mr. David Bentley, Research Technologist, and Dr. Arthur Cohen, Director, Electron Microscope Center, Washington State University, for the scanning electron micrographs.

Literature Cited

Borchardt, G. A., M. E. Harward, and R. A. Schmitt. 1971. Correlation of volcanic ash deposits by activation analysis of glass separates. Quat. Res. 1: 247-260.

Crandell, D. R., D. R. Mullineaux, R. D. Miller, and M. Rubin. 1962. Pyroclastic Deposits of Recent Age at Mount Rainier, Washington. U.S. Geol. Surv. Prof. Paper 450-D. Pp D64-D68.

Dudas, M. J., M. E. Harward, and R. A. Schmitt. 1973. Identification of dacitic tephra by activation analysis of their primary mineral phenocrysts. Quat. Res. 3: 307-315.

Mullineaux, D. R. 1964. Extensive Recent Pumice Lapilli and Ash Layers from Mount St. Helens Volcano, Southern Washington (Abstract). Geol. Soc. Amer. Spec. Paper 76. P. 285.

Okazaki, R., H. W. Smith, R. A. Gilkeson, and J. Franklin. 1972. Correlation of West Blacktail ash with pyroclastic layer T from the 1800 A.D. eruption of Mount St. Helens. Northwest Sci. 46: 77-89.

Randle, K., G. G. Goles, and L. R. Kittleman. 1971. Geochemical and petrological characterization of ash samples from Cascade Range volcanoes. Quat. Res. 1: 261-282.

Smith, H. W., R. Okazaki, and J. Aarstad. 1968. Recent volcanic ash in soils of northeastern Washington and northern Idaho. Northwest Sci. 42: 150-160.

Smith, D. G. W., and J. A. Westgate. 1969. Electron probe technique for characterising pyroclastic deposits. Earth and Planetary Sci. Letters 5: 313-319.

————, J. A. Westgate, and M. C. Tomlinson. 1969. Characterisation of pyroclastic units—a stratigraphic application of the microprobe. Proc. 4th Natl. Conf. on Electron Microprobe Analysis, Paper 34.

Westgate, J. A., and Gold, C. M. (editors). 1974. World Bibliography and Index of Quaternary Tephrochronology. Printing Services Department, The University of Alberta, Edmonton, Alberta, Canada. 528 p.

————, D. G. W. Smith, and M. Tomlinson. 1970. Late Quaternary Tephra Layers in Southwestern Canada. Proc. 2nd Annual Paleo-environmental Workshop of the University of Calgary Archaeological Association. The Students' Press, Calgary, Alberta, Canada. Pp. 13-34.

Received April 4, 1975.
Accepted for publication May 9, 1975.

Earl E. Krygier[1]
and
Howard F. Horton
Department of Fisheries and Wildlife
Oregon State University
Corvallis, Oregon 97331

Distribution, Reproduction, and Growth of Crangon nigricauda and Crangon franciscorum in Yaquina Bay, Oregon[2]

Abstract

The distribution, reproduction, and growth of *Crangon nigricauda* (*C.n.*) and *C. franciscorum* (*C.f.*) in Yaquina Bay, Oregon, are described based on the examination of 8244 *C.n.* and 4568 *C.f.* collected by beam trawl at bimonthly intervals from December 1970 through February 1972.

The distribution of *C.n.* and *C.f.* is generally related to water temperature and salinity. Both species exhibit a wide tolerance for temperature (5.2-16.5 C for *C.n.* and 5.3-21.5 C for *C.f.*) and salinity ($\geq$19 ppt for *C.n.* and 0.2-34.4 ppt for *C.f.*). Between species, *C.n.* displays a greater preference for cooler temperature and higher salinity than does *C.f.* Within species, variations in response to temperature and salinity changes were observed between size and sex groupings.

The spawning season for both species is from December to mid-August, and ovigerous females disappear from the bay in September (*C.n.*) and August (*C.f.*). Berried females were collected in waters ranging from 6.8 to 12.9 C for *C.n.* and from 6.8 to 19.2 C for *C.f.*, and with salinity of $\geq$ 25.4 ppt for *C.n.* and $\geq$ 14.6 ppt for *C.f.* Both species exhibit bimodal spawning periods with larger females spawning earliest. Fecundity is correlated ($R^2 \geq .91$) with total length (TL), with the mean and range being 4016 and 2393-7000 ova for *C.n.* and 3528 and 1923-4764 ova for *C.f.*

Growth of young was defined by the regression equations: $Y = -6.04 + 0.76$ (TL) summer and $Y = +7.79 + 0.95$ (TL) winter for *C.n.* Only a summer growth rate was estimated for *C.f.* with the regression equation being $Y = -25.44 + 1.37$ (TL). Both species exhibited differential growth after attaining sexually recognizable sizes, with females being 8-10 mm TL larger than males at maturity. Females apparently live a maximum of 1-1/2 yr and males not more than 1 yr.

Introduction

Crangon nigricauda (Stimpson) and *C. franciscorum* (Stimpson) comprise the major portion of epifaunal decapod shrimp in Yaquina Bay, Oregon. Such crangonids (=cragonid [Holthuis, 1951]) are important in estuaries because they often predominate in the diet of sport and marketable fishes (Herdman, 1904; Meredith, 1952; Daiber, 1959; Allen, 1960; Hess, 1961; Haertel and Osterberg, 1966; Makarov, 1966). Agitation of bottom sediments in the shrimp's search for food and protection and the frequency of molts (Lloyd and Yonge, 1947) contribute to the cycling of nutrients. Because estuaries are endangered habitats (Rudy, 1970), we conducted this study to provide new knowledge for conservation of these ecologically important species.

Several investigations have been conducted on the distribution and biology of crangonids outside Oregon. Rathbun (1904) reported that *C. nigricauda* (*C.n.*) is distributed from Comox, British Columbia, to Lower California at depths ranging from 3 to 31 f; and that *C. franciscorum* (*C.f.*) is distributed from southeastern

[1] Present address: School of Oceanography, Oregon State University, Corvallis, Oregon 97331.
[2] Research supported by NOAA (U.S. Department of Commerce) Institutional Sea Grant #04-3-158-4.

Alaska to San Diego, California, at depths ranging from about 1 to 29 f. Schmitt (1921) reported that *C.n.* may occur as far north as Alaska and as far west as Japan.

Isreal (1936) and Bonnet (1932) discussed the life history and commercial fishery for both species in San Francisco Bay, California. Haertel and Osterberg (1966), in their study of the lower Columbia River, noted the distribution of *C.f.* within the estuary and provided information on its place in the food web.

Much information on these shrimp was interpreted from studies of other species. Allen (1960, 1966) discussed the migration, reproductive biology, growth, and feeding habits of *Crangon allmani* and *C. vulgaris* in Northumberland waters of England. Meredith (1952) described growth, size distribution, and migration of *C. vulgaris* in the Liverpool Bay area of England. She also described development of the ovary and ovum as well as morphological changes in the reproductive cycle of both sexes. Other aspects of the biology of *C. vulgaris* were studied in Bristol Channel and Severn Estuary by Lloyd and Yonge (1947). Price (1962) defined growth rates, reproductive potential, and food habits of *C. septemspinosa* in the Delaware Bay region of Maryland. The larval forms of several species of Crangonids were described by Lebour (1931), Needler (1941), and Loveland (1968).

Methods and Materials

We captured crangonids from December 1970 through February 1972 at four sampling stations in Yaquina Bay (Fig. 1) using a 63-in wide by 22-in high beam trawl (Fig. 2). The trawl net had a body liner of 3.5 mm stretch mesh, and a cod-end liner of 1.5 mm stretch mesh. For each sample we towed the trawl for 15 minutes at 4:1 scope in mid-channel where bottoms consisted of soft sand and shells, except at station No. 4 where decaying wood and leaves comprised the major sediments. Mean depth at the sampling sites was 14, 9, 7, and 4 meters for station Nos. 1, 2, 3, and 4, respectively. We determined the distance the trawl traveled along the bottom by use of a 1 m (circumference) wheel and revolution counter attached to one skid (Fig. 2).

We collected shrimp and data on water depth, salinity, and temperature every 14 days, when possible, for the 15-month study. From each tow we placed a random sample of shrimp (ca. 150) in 10% buffered formalin (later transferred to 35% isopropyl alcohol) and estimated the remaining number of animals.

From the 119 collections, we measured (nearest 0.1 mm) 4568 *C.f.* and 8244 *C.n.* from the tip of rostrum to the tip of telson for total length (TL). We arithmetically averaged these lengths into 2 mm groups with odd lengths placed with the next lower interval. The frequency of observations of the mean lengths for each 2 mm interval was used to compute a weighted mean length (Krygier, 1974) for each age and sex grouping for each sampling station on each sampling day. Sexually unidentifiable shrimp were placed with identifiable, but sexually immature males and females, on a 50:50 ratio. Such placement was based on the results of sampling which indicated that the sex ratio of sexually immature shrimp was 50:50 (Wenner, 1972).

Using statistical analyses of the distributional changes for the two species of shrimp, and the correlation of these changes with hydrographic data, we described the patterns of migration within the bay system. Because of the large inherent variation within the sampling procedure and the number of variables observed, the resultant R^2 and F-tests for significance of regression (Draper and Smith, 1966) yield only general trends in

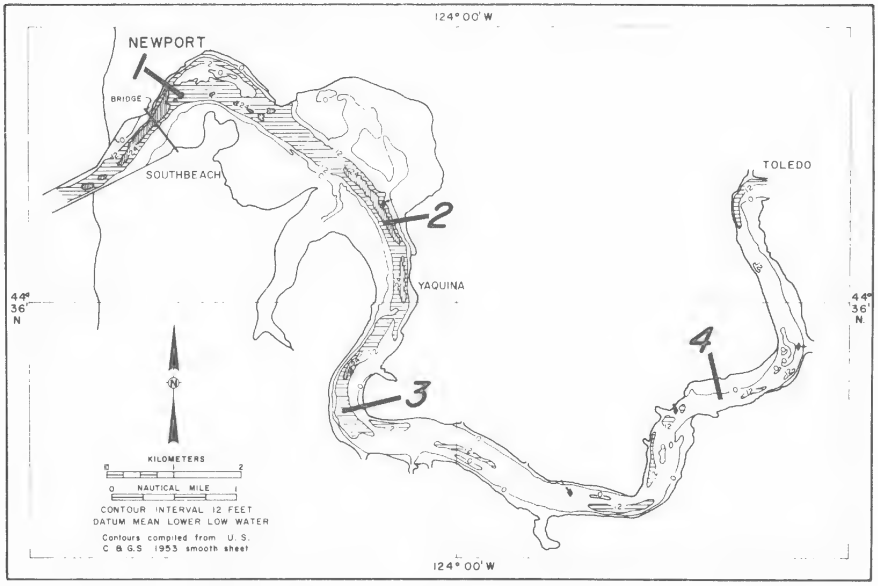


Figure 1. Map of Yaquina Bay, Oregon, showing the four sampling stations where Crangonid shrimp were collected from December 1970 through February 1972.

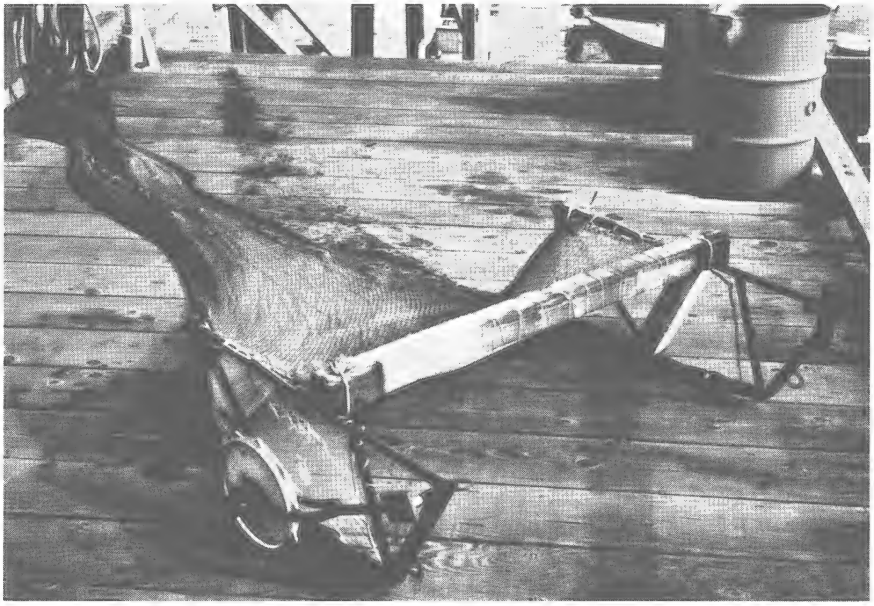


Figure 2. Beam trawl, with attached 1-m wheel, used to capture Crangonid shrimp in Yaquina Bay, Oregon.

migration patterns. R^2 values were statistically low, but the F-tests indicated significant relationships of temperature, salinity, and temperature-salinity interaction on the distribution of numbers and size of shrimp.

We determined the sex of all specimens by microscopic examination of: (1) The endopodite of the first pleopod which is short and curved inward for males, and long and straight for females (Lloyd and Yonge, 1947; Meredith 1952). (2) The endopodite of the second pleopod which on developing and mature males bears an appendix masculina, whereas for females the structure is similar to those on the first and third pleopod (*Ibid.*). (3) The location of the gonopore which is at the base of the fifth pair of walking legs in males and at the base of the third pair of walking legs in females. Using a combination of these characteristics we determined the sex of specimens $\geqq$22 mm for *C.n.* and $\geqq$26 mm for *C.f.*

We determined sexual maturity from squashes of testes (Feulgen squash method for testes [Darlington and LaCour, 1969]) and squashes of ovaries (untreated) examined under a phase-contrast microscope. The presence of sperm indicated maturity for males and the presence of ova on the egg pad or ripe ovaries (stage 7 condition described and illustrated by Meredith [1952]) indicated maturity for females.

We used the method of Price (1962) to determine the relationship between fecundity and TL. We measured eggs from each mass (pad) for their largest diameter, and inspected them to determine stage of development. The four stages of egg development used were patterned after those described by Meredith (1952). To minimize the effect of possible egg loss during incubation or handling, we enumerated only those ova in early developmental stages (A and B) for determination of fecundity relationships. For fecundity determinations, we stripped and enumerated the eggs of 15 ovigerous females of each species ranging in size from 41.0 to 61.4 mm for *C.n.* and 47.8 to 67.4 mm for *C.f.*

For growth determinations we analyzed the length-frequency distributions of the sexually unrecognizable pre-adult males and females combined, and the sexually recognizable males and females independently. The collections from the four sampling stations were pooled according to the date of collection. We estimated the growth rates of the pre-adults by regressing the modal peaks of length-frequency distributions on the numerical value of the week in question.

Results

Distribution

C. nigricauda. The young (immature) and adults of *C.n.* show a general trend of decreasing in abundance with increasing water temperature; ovigerous females, however, give a non-significant response to temperature (Table 1). Temperature values over the sampling period at each station are plotted in Figure 3, and changes in abundance of shrimp at each sampling station are plotted in Figures 4 and 5. The range of temperatures where immature *C.n.* were collected is 6.5-16.5 C; for adults the range is 5.2-16.5 C. Ovigerous females were collected in water ranging from 6.8 to 12.9 C, with 94% found between 8-11 C (Fig. 3, Table 2).

A slight increase in numbers of *C.n.* is associated with increasing salinity; the effect on all age classes is significant (F-test) at the 1% level (Table 3). The distribution of immature shrimp is more greatly affected by changes in temperature and salinity

TABLE 1. Slope and R^2 values describing the relationship of temperature to size (length) and abundance (frequency) of each age and sex group of *Crangon nigricauda* and *C. franciscorum* in Yaquina Bay.

Variables	Slope	R^2
	C. nigricauda	
Temperature-frequency		
immature males	−2.646*	.055
immature females	−3.384**	.060
mature males	−1.195*	.048
mature females	−0.577*	.051
ovigerous females	−0.092	.013
Temperature-size		
immature males	−0.766*	.062
immature females	−0.944*	.073
mature males	−1.794**	.132
mature females	−2.603**	.126
ovigerous females	−0.063	.015
	C. franciscorum	
Temperature-frequency		
immature males	+2.996**	.354
immature females	+3.010	.181
mature males	−0.185	.002
mature females	−0.757**	.098
ovigerous females	−0.015	.001
Temperature-size		
immature males	+0.874*	.061
immature females	−0.535	.021
mature males	−0.168	.003
mature females	−1.434*	.068
ovigerous females	+0.446**	.113

* F-statistic significant at 5% level.
** F-statistic significant at 1% level.

than is that of the adults. The salinity values at each sampling station are plotted in Figure 3. With few exceptions, *C.n.* normally were observed in waters with >19 ppt salinity (Figs. 3, 4, 5). Ovigerous females were not seen in water <25.4 ppt and most occurred in water ≥32 ppt (Fig. 3, Table 2), with 34.5 ppt being the maximum salinity observed in the bay.

The regression of size of individuals against temperature indicates that larger animals appear to leave an area with increasing temperature, and as a result the likelihood of finding smaller individuals increases (Table 1). Salinity has the opposite effect of temperature. Here, increases in salinity are associated with the occurrence of larger individuals in an area. Consequently, smaller shrimp tend to occur up-bay in the less saline waters of station No. 3. The hydrographic factors which most strongly affect the adult population appear to be temperature in the summer and salinity in the winter.

The fact that both temperature and salinity independently affect the distribution of these shrimp is shown in their interaction regression on numbers and size (Table 4). This temperature-salinity (T-S) interaction shows an increase in the R^2 values greater than the sum of the two variables (Mendenhall, 1963). The result of the T-S interaction seems to limit *C. nigricauda* to the three down-bay collection sites where influence of the oceanic environment produces relatively high salinity and low temperature (Fig. 3). High temperatures help to explain the disappearance of adults from station Nos. 2 and 3 from June-October, and the decrease in numbers at station No. 1 in early

TABLE 2. Number of ovigerous *Crangon nigricauda* in Yaquina Bay, Oregon, by sampling station (St#), date of collection, and stage of egg development.

Date	A-Stage Egg*			B-Stage Egg			C-Stage Egg			D-Stage Egg		
	St# 1	St# 2	St# 3	St# 1	St# 2	St# 3	St# 1	St# 2	St# 3	St# 1	St# 2	St# 3
1-11-71		1										
1-18-71	3						1			1		
1-25-71												
3- 1-71	4									1		
3-15-71												
3-29-71	4						1			1		
4-12-71	1			1								
5- 7-71				1								
5-21-71	2			2								
6- 6-71	4			3			1					
6-18-71	4			2			1					
7- 2-71	1		2	11			3					
7-16-71	2			5			2					
7-30-71		1		5			1			1		
8-13-71	1			1			1			7		1
8-27-71				5						3		
9-10-71												
9-24-71				1								
12-17-71	1											
12-30-71	3			6								
1-14-72				1								
1-28-72	2			1								
2-11-72												
2-25-72	3			2			3					

* From Meredith (1952).

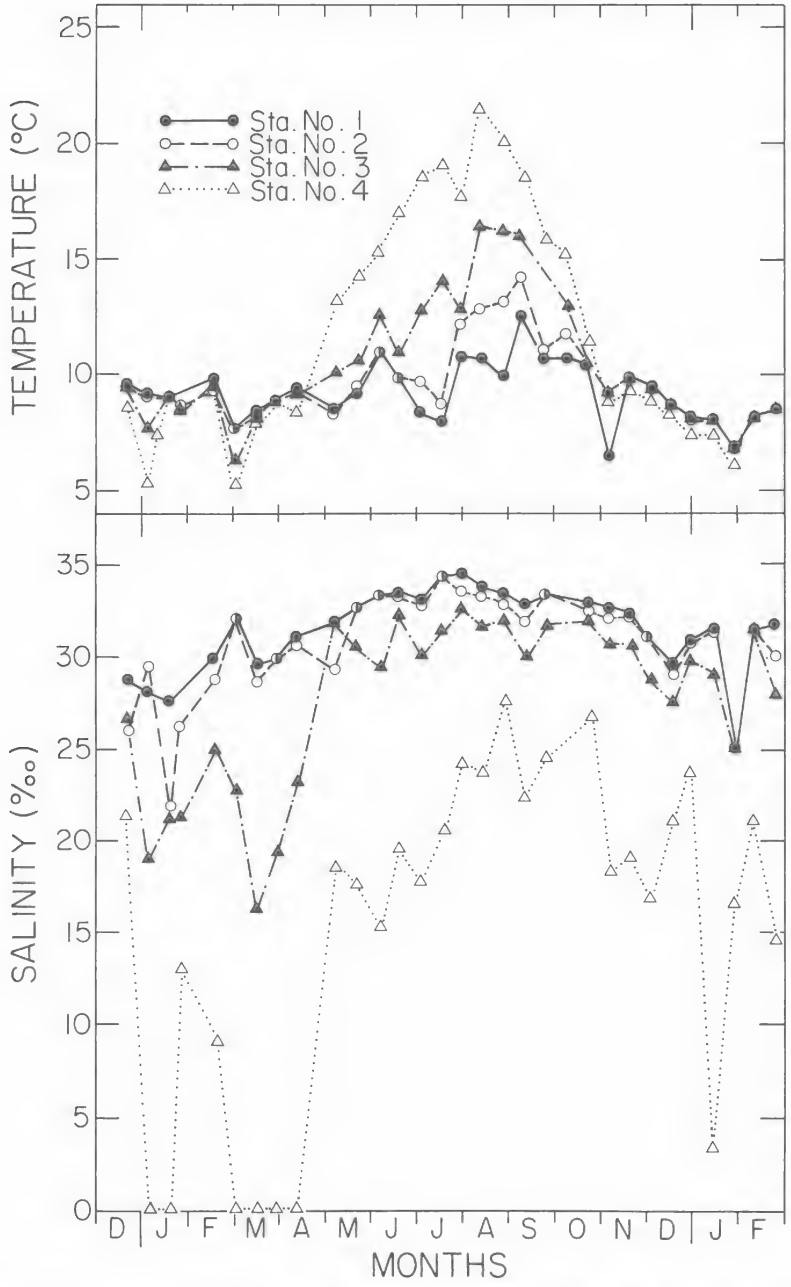


Figure 3. Temperature and salinity values by date of collection at four *Crangon* sampling stations in Yaquina Bay, Oregon, 1970-1972.

September (Figs. 4, 5). There is a corresponding increase in shrimp abundance as temperatures decrease in the fall.

Much of the apparently contradictory peaks and dips in the graphs of abundance (Figs. 4, 5) are attributed to recruitment of new age classes (Fig. 6), and possibly to an influx of animals from the marine environment west of station No. 1.

C. franciscorum. The abundance of young *C.f.,* unlike *C.n.,* shows a positive reaction to water temperature (Table 1). A slight reverse effect is seen with adult females. The effects of temperature on abundance of adult males and ovigerous females are not significant (Table 1). The temperature range for occurrence of young and adult *C.f.* was 5.2-21.3 C, and for ovigerous females was 6.8-19.2 C.

The effect of salinity on abundance of *C.f.* is negative, with young females showing the greatest response to salinity followed by young males (Table 3). The negative effect of salinity on abundance of adults is most pronounced when salinity is <5 ppt (Figs. 3, 8). The ranges of salinity for young and adult *C.f.* were 0.2-34.4 ppt. Ovigerous females showed a positive response to salinity (Table 3) and were obtained only in waters >14.6 ppt.

In *C.f.* the temperature-size relationship is positive for young males and ovigerous females, and negative for young and adult females (Table 1). The salinity-size relationship for young and adults is negative for all but ovigerous females (Table 3). Responses of non-ovigerous adults to changes in salinity are not significant at the 5%

TABLE 3. Slope and R^2 values describing the relationship of salinity to size (length) and abundance (frequency) of each age and sex group of *Crangon nigricauda* and *C. franciscorum* in Yaquina Bay.

Variables	Slope	R^2
	C. nigricauda	
Salinity-frequency		
immature males	+1.243**	.086
immature females	+1.848**	.127
mature males	+0.605**	.087
mature females	+0.258**	.072
ovigerous females	+0.084**	.075
Salinity-size		
immature males	+0.789**	.487
immature females	+0.675**	.260
mature males	+0.998**	.274
mature females	+1.398**	.253
ovigerous females	+0.843**	.112
	C. franciscorum	
Salinity-frequency		
immature males	−0.570**	.093
immature females	−1.330**	.253
mature males	−0.254	.027
mature females	−0.270**	.089
ovigerous females	+0.017	.006
Salinity-size		
immature males	−0.906**	.341
immature females	−0.911**	.176
mature males	−0.279	.015
mature females	−0.368	.044
ovigerous females	+0.821**	.158

**F-statistic significant at 1% level.

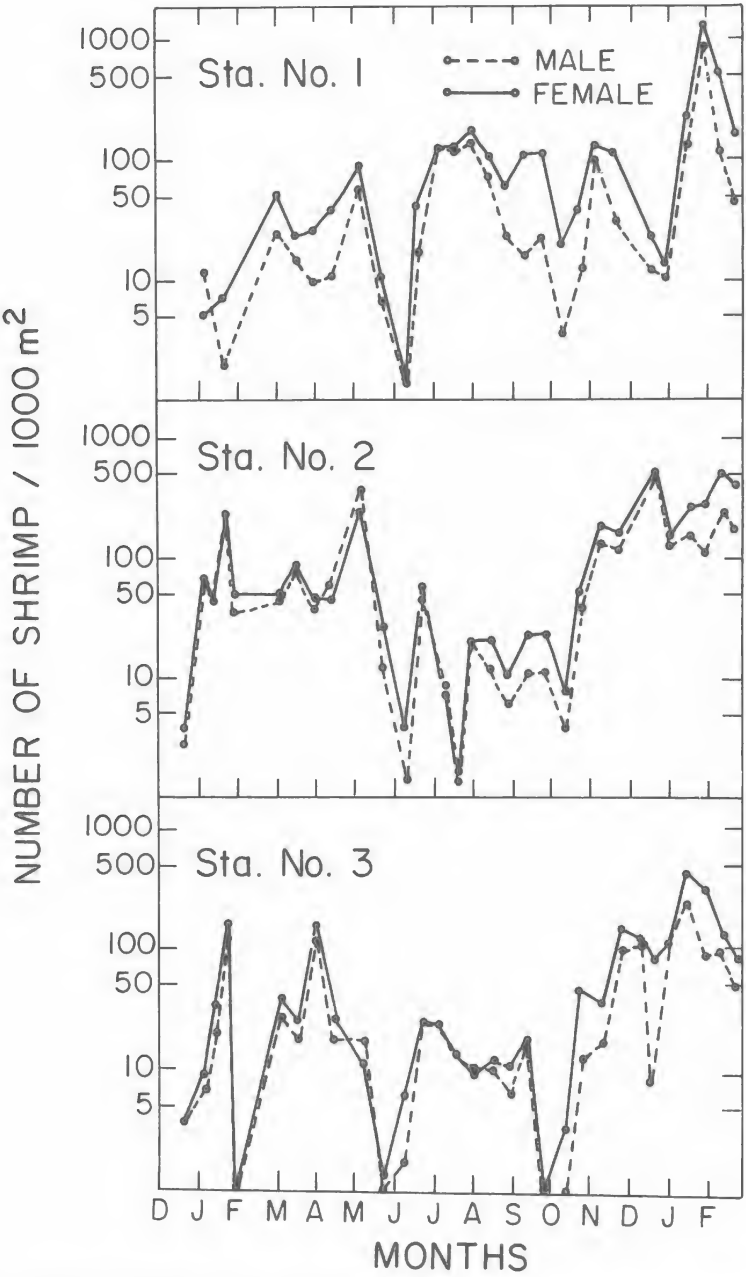


Figure 4. Relative abundance and date of collection of sexually immature *Crangon nigricauda* from three sampling stations in Yaquina Bay, Oregon, 1970-1972.

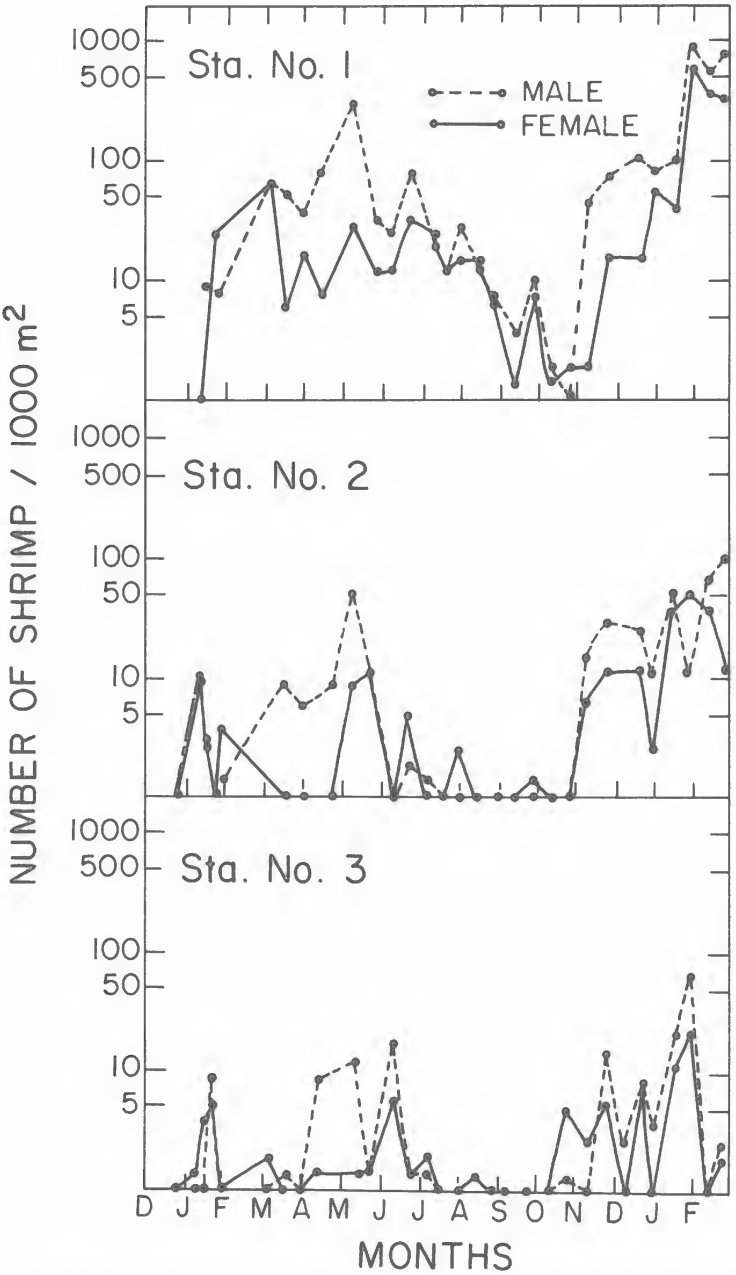


Figure 5. Relative abundance and date of collection of sexually mature *Crangon nigricauda* from three sampling stations in Yaquina Bay, Oregon, 1970-1972.

TABLE 4. Slope and R^2 values describing the relationship of the temperature-salinity (T-S) interaction to size (length) and abundance (frequency) of each age and sex group of *Crangon nigricauda* and *C. franciscorum* from Yaquina Bay.

Variables	Slope (temp.)	Slope (salinity)	R^2
	C. nigricauda		
T-S-frequency			
immature males	−3.051**	+1.39	.156
immature females	−4.028**	+2.04	.208
mature males	−1.456**	+0.67	.154
mature females	−0.682**	+0.29	.140
ovigerous females	−0.122**	+0.09	.097
T-S-size			
immature males	−0.776**	+0.80	.552
immature females	−0.984**	+0.69	.335
mature males	−1.859**	+1.02	.398
mature females	−2.598**	+1.43	.371
ovigerous females	−0.655**	+0.85	.132
	C. franciscorum		
T-S-frequency			
immature males	+3.260**	−0.73	.500
immature females	+3.525**	−1.50	.491
mature males	−0.113	−0.25	.027
mature females	−0.680**	−0.24	.164
ovigerous females	−0.016**	+0.02	.006
T-S-size			
immature males	+0.930**	−0.92	.388
immature females	−0.508**	−0.90	.184
mature males	−0.089	−0.28	.016
mature females	−1.422*	−0.35	.074
ovigerous females	+0.454**	+0.81	.160

* F-statistic significant at 5% level.
** F-statistic significant at 1% level.

level (Table 3). Overall, salinity appears to be more important than temperature in causing changes in abundance of *C.f.*

The T-S interaction indicates that both variables influence changes in the distribution of *C.f.* (Table 4). The interaction effect is seen most clearly in immatures, where high salinity of water usually retards down-bay migration, whereas increases in temperature during the summer favor movement into these waters. The result of these hydrographic influences is that *C.f.* thrives on the fringe of the oceanic environment (Figs. 3, 7, 8).

Reproduction

C. nigricauda. During the breeding season, 95% (N=110) of *C.n.* females were mature at $\geq$40 mm TL, and either had eggs on the egg pad or a stage 7 ovary. The mean TL of the 115 ovigerous females sampled was 49.3 mm, and the range was 36.2-61.4 mm.

For males, 88.3% (N=60) were mature at 28 mm TL, 8.3% were mature at 26 mm, and 3.3% >28 mm contained no ripe sperm. The sperm of *C.n.* and *C.f.* is similar in appearance to that described by Kume and Dan (1957) for natiantian shrimp.

The spawning season for *C.n.* within the bay system is from December to mid-

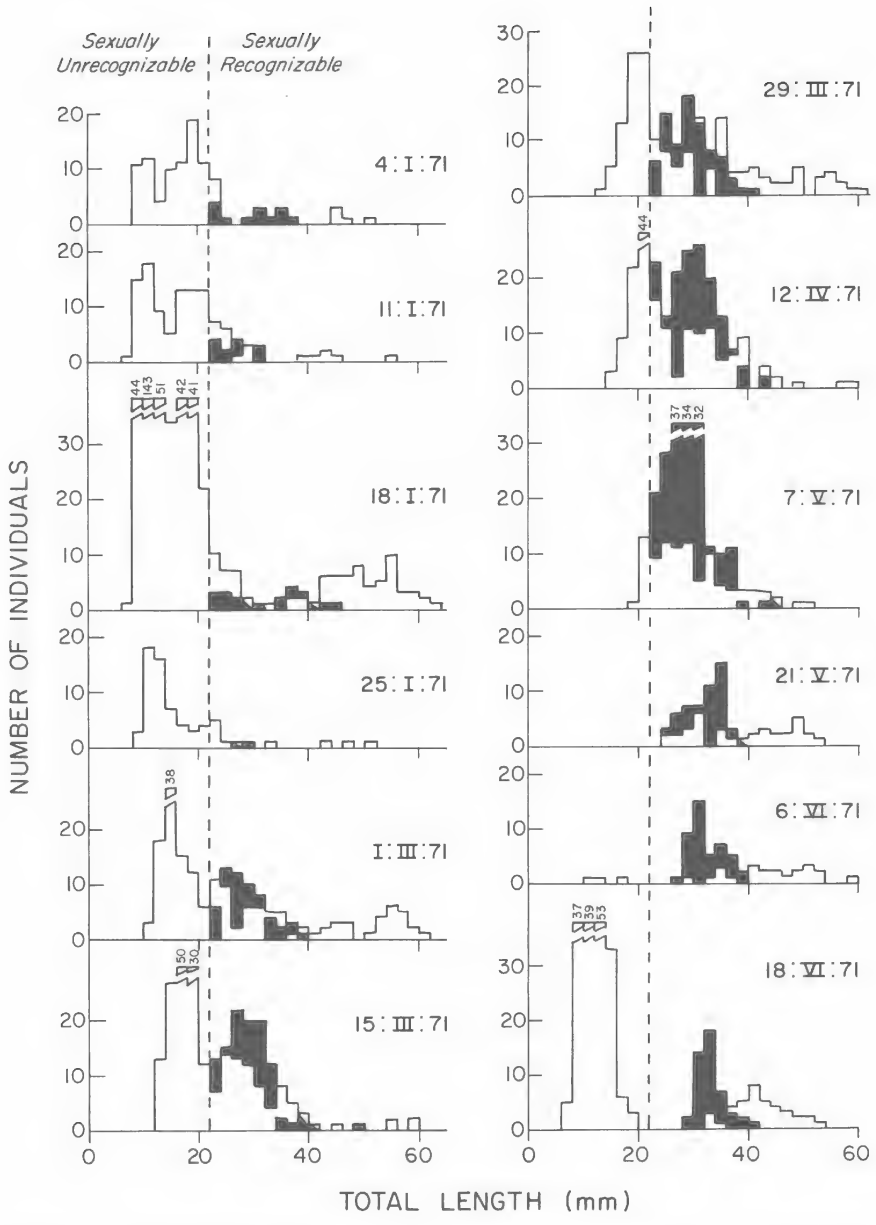
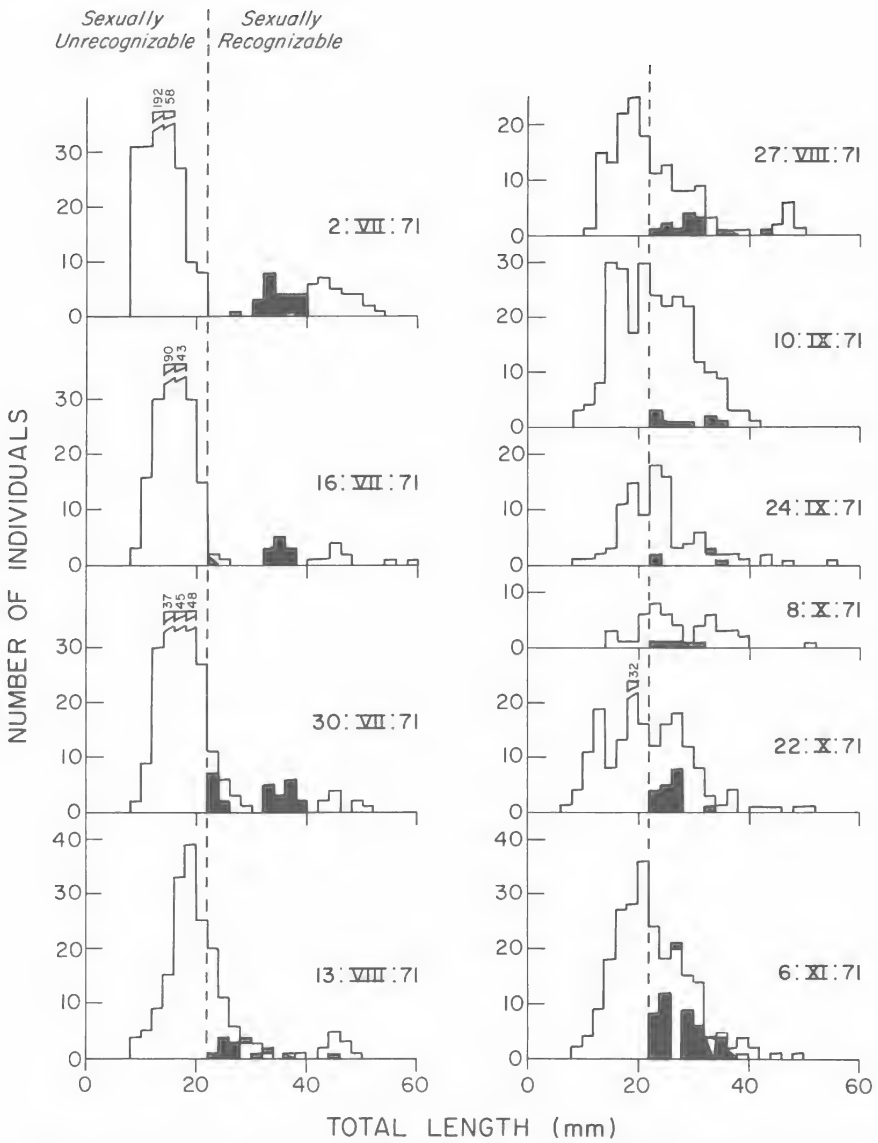


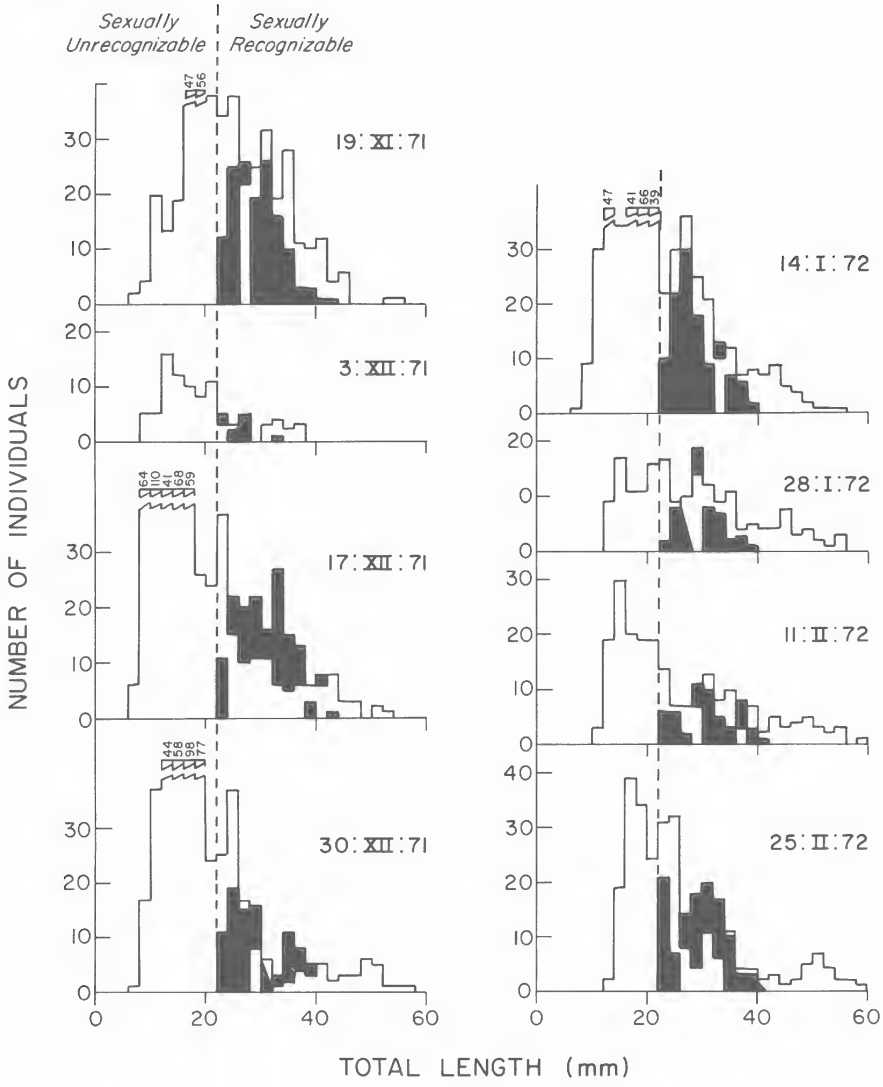
Figure 6. Length-frequency histograms of sexually unrecognizable (<22 mm TL) and sexually recognizable (22 mm TL) *Crangon nigricauda* in Yaquina Bay, Oregon, 1971-1972. Data pooled for all sampling stations by date of capture. For sexually recognizable shrimp, solid bars=males, and open bars=females.

Figure 6 (b)



August as evidenced by the presence of A-stage eggs (Table 2) which are laid soon after copulation (Lloyd and Yonge, 1947). Two spawning peaks occur within this season as indicated by the bimodal curve of recruitment to the population (Fig. 6). The first peak occurs during December-March, when 88% of the ovigerous females are large ($\geqq$47 mm TL) and presumably older individuals. The second peak occurs from mid-May to mid-August, and consists of both small and large individuals. The

Figure 6 (c)



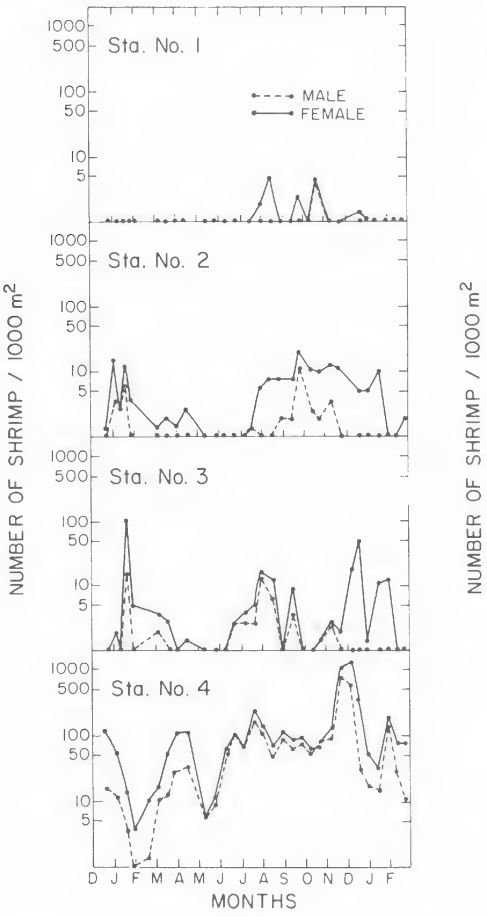
large females most likely are repeat spawners from the first peak of the year (Table 5). The second spawning appears to involve a larger number of individuals (Table 2).

An apparent spawning migration occurs from mid-September to December as evidenced by the "disappearance" from the area of abundance (station No. 1) of ovigerous females whose eggs had not fully developed (Table 2). All but 5 of the 115 ovigerous females were collected at station No. 1.

The reproductive potential for *C.n.* is described by $Y = -5878.9 + 200.7$ (TL), where Y is the fecundity of a shrimp of a given size, −5878.9 is the intercept, +200.7

is the slope of the regression line, and (TL) is the length of the female in question. The R^2 value is 0.91. The observed range of fecundity was 2393-7000 eggs for 43.2 and 60.2 mm females, respectively. Based on the regression equation, the largest female would carry 6443 eggs and the smallest 1386 eggs. The mean number of eggs per female is about 4016. Consequently, the spawning peak during December-March, which consists of relatively few but large individuals, actually contributes a significant proportion of eggs to the population as illustrated by the substantial recruitment of young in July (Fig. 6).

C. franciscorum. Sexual maturity for 98% (N = 110) of female *C.f.* occurred at about 48.0 mm with most incubating eggs or having a stage 7 ovary during the breeding



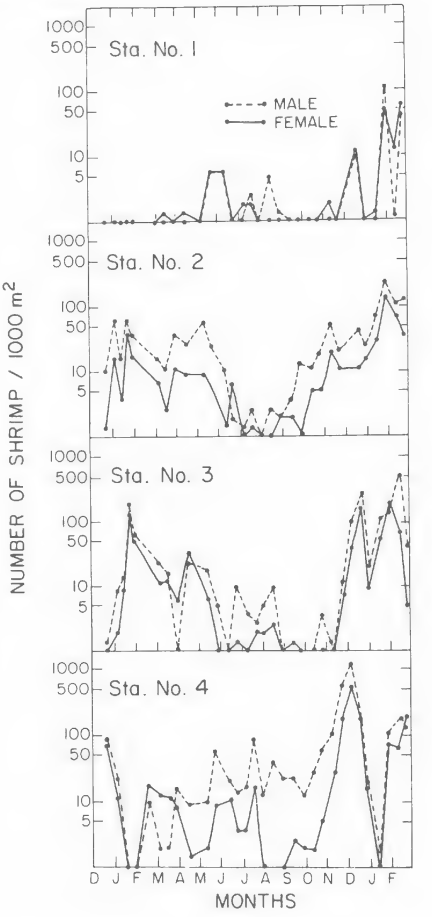


Figure 7. Relative abundance and date of collection of sexually immature *Crangon franciscorum* from four sampling stations in Yaquina Bay, Oregon, 1970-1972.

Figure 8. Relative abundance and date of collection of sexually mature *Crangon franciscorum* from four sampling stations in Yaquina Bay, Oregon, 1970-1972.

season. The mean and range of lengths for the 120 ovigerous females captured was 56.8 mm and 43.6-68.8 mm TL, respectively. Most males were mature at 34.0 mm TL.

The spawning season for *C.f.* is bimodal and occurs from December to mid-August (Fig. 9, Table 6). As with *C.n.*, the larger and presumably older females appear during December-March, when only 5% of those with eggs were <55 mm TL (Table 7). The second and largest period of spawning, April to mid-August, included both incoming and repeat spawners (Fig. 9, Table 6).

A "spawning migration" of these normally low-saline-inhabiting shrimp is indicated by the occurrence of ovigerous females in high-salinity waters of the lower bay. This was the case for all but 10.8% of the 120 ovigerous females collected (Table 7, Fig. 3). Peaks in the abundance of females which coincide with spawning activity appear when waters of the lower three collection stations are increasing in salinity during March-July and at station No. 4 during June-July (Fig. 8, Table 7). Ovigerous females are present during the first peak, when salinity is >21 ppt, and during the second peak, when salinity is $\geqq 30$ ppt (except for one collection) in the lower three collection sites. At station No. 4 only one ovigerous female was captured outside the May-July period when salinities were <14.8 ppt. The males appear to migrate with the females during the spawning season. As with *C.n.* there is a "disappearance" of ovigerous females whose eggs were not fully developed during mid-August to December.

The reproductive potential for *C.f.* is described by $Y = -5338.7 + 156.1$ (TL), with $R^2 = .95$. The observed range of fecundity was 1923-4764 eggs for 47.8-67.4 mm TL females, respectively. Based on the regression equation, the range of fecundity is 1467-5401 eggs, with a mean of 3528 eggs.

TABLE 5. Frequency, location, and date of capture of small (<47 mm TL) and large (≥ 47 mm TL) ovigerous *Crangon nigricauda* collected in Yaquina Bay.

	Station #1		Station #2		Station #3	
Date	Small	Large	Small	Large	Small	Large
1-11-71				1		
1-18-71		5				
3- 1-71		5				
3-29-71		6				
4-12-71		2				
5- 7-71		1				
5-21-71		4				
6- 6-71	1	7				
6-18-71	1	6				
7- 2-71	10	5			1	1
7-16-71	6	3				
7-30-71	5	2	1			
8-13-71	7	3			1	
8-27-71	4	4				
9-24-71		1				
12-17-71	1					
12-30-71	2	7				
1-14-72	1					
1-28-72		3				
2-25-72	1	7				

TABLE 6. Capture point (station number [St#]), date of collection, number of specimens, and stage of egg development of ovigerous *Crangon franciscorum* collected in Yaquina Bay.

	A-Stage Egg				B-Stage Egg				C-Stage Egg				D-tSage Egg			
Date	St# 1	St# 2	St# 3	St# 4	St# 1	St# 2	St# 3	St# 4	St# 1	St# 2	St# 3	St# 4	St# 1	St# 2	St# 3	St# 4
1- 4-71		1				1										
1-11-71			1													
1-18-71		4	5				1									
1-25-71		4	1													
3- 1-71		1				1										
3-15-71							1									
3-29-71		4				1										
4-12-71		3	14		1						1			1		
5- 7-71		1	2	1		2										
5-21-71				1	3								2			
6- 6-71				3	2	1			1				2			
6-18-71				1		1								2	1	
7- 2-71				1									2			2
7-16-71				3	1									1	1	
7-30-71			1				1								2	
8-13-71			1				2								1	
12-17-71	2															
12-30-71		2	1													
1-14-72			1													
1-28-72	1	6	2								1					
2-11-72	1	2					3									
2-25-72	1	3		1	2											

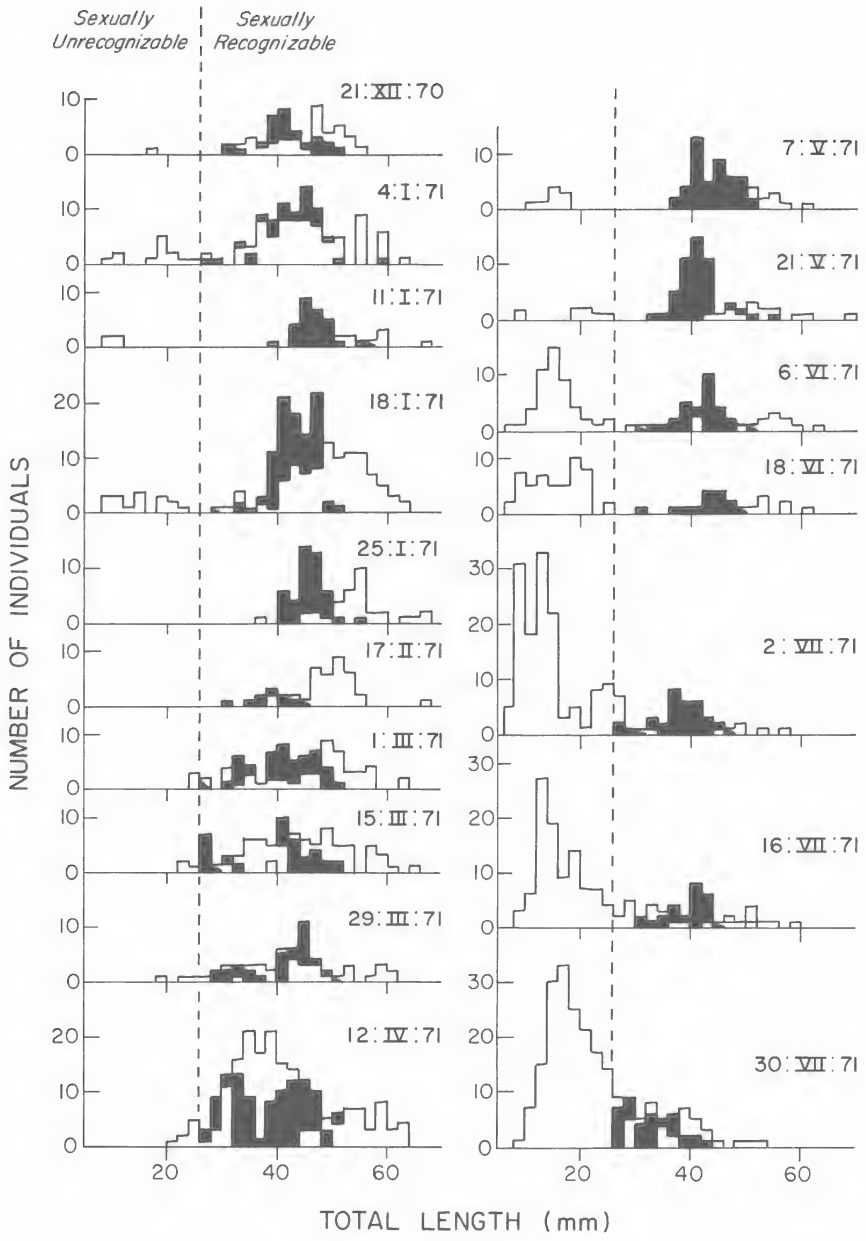
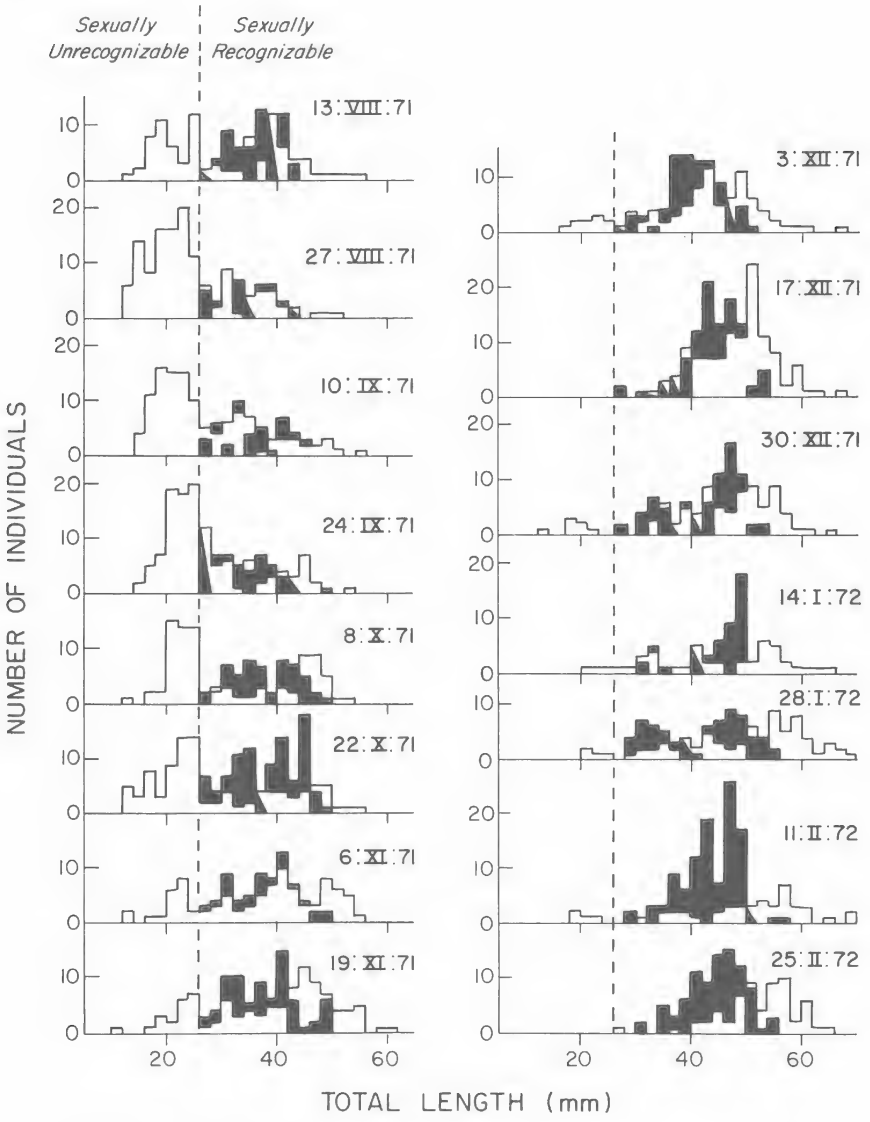


Figure 9. Length-frequency histograms of sexually unrecognizable (<26 mm TL) and sexually recognizable (26 mm TL) *Crangon franciscorum* in Yaquina Bay, Oregon, 1970-1972. Data pooled for all sampling stations by date of capture. For sexually recognizable shrimp, solid bars=males, and open bars=females.

Figure 9 (cont.)



In both *C.n.* and *C.f.*, we noted some females with apparent A-stage eggs in which ova were broken and the whole pad was disintegrating. Most appear to be the result of unsuccessful fertilizations and subsequent degeneration of the egg pad (Lloyd and Yonge, 1947).

Repeat spawning was demonstrated in both species by the presence of ovarian stages 5-7 in females early in the spawning season which also had eggs on their egg

TABLE 7. Data showing the frequency, location, and date of capture of small (<55 mm TL) and large (>55 mm TL) ovigerous *Crangon franciscorum*, and the percent of mature females bearing eggs in Yaquina Bay.

	Station #1			Station #2			Station #3			Station #4		
Date	Small	Large	%	Small	Large	%	Small	Large	%	Small	Large	%
1- 4-71				2		16.7						
1-11-71								1	16.7			
1-18-71					4	18.2		6	15.0			
1-25-71				1	3	23.5		1	8.3			
3- 1-71					2	33.3						
3-15-71								1	8.3			
3-29-71				1	4	62.5						
4-12-71		1	100.0		4	44.4	4	11	46.7			
5- 7-71				1		100.0	2	2	50	1		50.0
5-21-71	1	4	83.3							1		20.0
6- 6-71	2	3	100.0		1	100.0				3		60.0
6-18-71				2	1	50.0	1		100.0		1	100.0
7- 2-71		2	100.0							2	1	75.0
7-16-71	1		100.0		1	100.0		1	100.0	3		60.0
7-30-71							4		100.0			
8-13-71							4		100.0			
12-17-71		2	22.2									
12-30-71					2	15.4		1	11.1			
1-14-72								1	8.3			
1-28-72		1	50.0		6	46.2		3	10.5			
2-11-72		1	100.0		2	16.7		3	60.0			
2-25-72		3	75.0		3	37.5					1	2.7

pad. The stage 7 ovary was seen only on ovigerous females with C- and D-type eggs and on pre-egg bearing mature females.

Argeia pugettensis, a bopyroidean branchial isopod (Richardson, 1905), was observed in female *C.f.* ≧31.4 mm TL from December to mid-June. The mean TL of infected females was 44.8 mm. Because none of the infected adult females was "in berry" during the normal spawning season, we concluded that the infection curtails egg production.

Growth

C. nigricauda. The bimodal recruitment (Fig. 6) of *C.n.* indicates two groups of shrimp with separate rates of growth. Group I is the product of the December-March spawning, the larvae of which are planktonic until about mid-June. The young grow steadily for a year when they mature and spawn (Table 2, Fig. 6). Along with this group of maturing shrimp is a group of large females which spawn in December-January (Table 5). Most of these large females are undoubtedly the remains of group II which spawned the previous summer and help initiate the group I spawning. The eggs of group I, by inspection of the modal peaks of the egg stages (Table 2), are apparently carried for 10-14 weeks before the larvae hatch into the plankton.

Growth rates for group I young (N = 14 weeks) during the summer are described by: $Y = -6.04 + 0.76\ (X)$. Where Y is the TL of the shrimp in mm, –6.04 is the intercept, +0.76 mm is the slope, and (X) is the week considered. Thus the growth of the young shrimp is approximately 0.76 mm per week. This equation holds for this group ($R^2 = .99$) until the shrimp are >22 mm, or about 15-16 weeks after the shrimp leave the plankton. Growth rate of females then appears to accelerate so that by maturity (December-March) females are 8-10 mm larger than males (Fig. 6).

Group II shrimp hatch during mid- to late summer (Table 2) and are planktonic until December, when they first appear in benthic samples. The young grow steadily until they reach spawning size from June to mid-August (Fig. 6). This spawning group consists of newly mature females (8-10 mm larger than males) and some large females (Table 5), which apparently are repeat spawners from group I. The eggs of this group are incubated 8-10 weeks (Table 2). Growth rate (January-June) of the young of group II (N = 15 weeks) is described by: $Y = +7.79 + 0.95\ (X)$, $R^2 = .99$, or about 0.95 mm per week.

The smallest juvenile was 6.6 mm, and the average size of the young leaving the plankton was 6.8-7.0 mm. Males are seldom >40 mm and probably spawn once and die. Females seldom exceed 55 mm (Fig. 6) by which time they must be approximately 1½ years old. The ratio of females to males was 1.35:1.00 (N=4123), but there was great variation of the ratio between collections. It appears that group I shrimp mature at a larger size than group II (Fig. 6, Table 5). Differential size at maturity is likely caused by slower growth of group I adults during winter.

C. franciscorum. The cycle of growth of the two species is similar. For *C.f.,* the eggs of group I hatch in the early spring (Table 6), develop into juveniles by May-July, and reach maturity in December (Fig. 9). The larger of these newly mature shrimp, plus a few large females (probably the remains of the group II females), begin spawning in mid-December. The remainder reach maturity and spawn in Februrary-March (Table 7, Fig. 9).

The young of group II hatch during mid- to late summer, and recruit to the population in December (Table 6, Fig. 9). Representatives of this recruitment (7-22 mm TL) are seldom seen, and they are assumed to be out of the sampling area. The maturing adults reach spawning size in summer. The largest members of the new group, plus the repeat spawners from group I, begin the spawning season near the end of May (Table 7, Fig. 9).

The incubation of group I eggs is not easily followed due to the lack of later stages in the samples (Table 6). They probably hatch in 10-12 weeks, while those of group II hatch in 8-10 weeks. The young of group I ($N = 16$ weeks) grow at a rate described by: $Y = -25.44 + 1.37$ (X), with $R^2 = .99$. Because the young of group II were not abundant within the sampling area, a growth equation was not possible. The smallest young was 6.8 mm, and post-larval shrimp are probably between 7.0–7.4 mm TL when they enter the population.

Differential growth of males and females is also evident and probably occurs after sexually recognizable size has been achieved (Fig. 9). Females apparently are 8-12 mm larger than males at maturity. Males normally do not exceed 50-52 mm, and females >62 mm are rare (Fig. 9). As with *C.n.*, females of the prespring spawning apparently mature at a larger size than those that spawn in summer (Table 7). The sex ratio for this species was 1.00:1.06 females to males (N=3555), though there was large variation among samples.

Discussion

Because *C.n.* and *C.f.* occur naturally in Yaquina Bay, the response of these animals to their environment indicates the adaptive ability of the two species to coinhabit the same body of water. Adult *C.n.* appear to inhabit the more oceanic environments of the bay (5.2-16.5 C and salinity 19.0-34.5 ppt; Figs. 3, 5), while smaller individuals are found in the warmer and less-saline water upbay (Tables 1, 3). This finding concurs with the observations of Israel (1936) who found the young of *C.n.* in the shallow, low-saline water of San Francisco Bay. Observations on similar species of crangonids indicate that the smaller the young the better the osmoregulatory mechanism (Isreal, 1936; Lloyd and Yonge, 1947; Allen, 1960, 1966). Broekema (1941, cited in Allen, 1966) saw an apparent relationship between salinity and age of shrimp, where the optimum salinity for a 1-year-old was 18-19 ppt at 22 C and for a 2-year-old was 28-29 ppt at 22 C. This situation helps explain why the older animals do not penetrate as far up the estuary as do the young.

C.f. is apparently more typical of a truly euryhaline species, withstanding ranges in temperature of 5.2-21.3 C and ranges in salinity of 0.2-34.4 ppt (Figs. 3, 8). Lloyd and Yonge (1947) and Allen (1966) state that, for euryhaline organisms, the ability to withstand salinity is influenced by temperature such that osmoregulation proceeds more efficiently at high temperature and may even be inhibited at low temperatures. The young of this species are also more tolerant of brackish water, and thus are abundant farther up the estuary than are larger and older individuals (Figs. 3, 7, 8).

Except for spawning migrations, the general trend is away from high-salinity water for this species. The overall T-S gradient appears to separate the two crangonid populations and their young and adult age classes in Yaquina Bay, thereby limiting competition between and within species.

For *C.n.,* the reproductive migration apparently includes an outbay migration to areas where the eggs can hatch in high-salinity water (Ehrenbaum, 1890, cited in Isreal, 1936, and Lloyd and Yonge, 1947). This out-migration, or "disappearance," is similar to that of *C. allmani* (Allen, 1960) where the ovigerous females disappeared at the height of the breeding season when many were bearing A- and B-stage eggs. The hypothesis that these shrimp migrated from the estuary is supported by results of an unrelated sampling program, located approximately 1 mile north and 1-3 miles off-shore from the estuary, in which numerous females were captured with eggs in an advanced C- and D-stage or whose eggs had recently hatched (Krygier, 1974). This condition may also be the case with *C.n.* of the early spring spawning, but the percentage of ovigerous females was small and the migration was not evident.

The spawning migration of *C.f.* is similar to that of *C.n.* in that the general movement is to deeper, more-saline water. Differences arise in the fact that the ovigerous females of this species do not require as high a salinity or as low a temperature regimen as do the ovigerous *C.n.* Because adults commonly live at salinities less than 15 ppt, the ovigerous females tend to be concentrated where salinity is at its maximum. A final movement from the estuary to cool, highly saline water is evidenced by the lack of females with C- and D-stage eggs which would be expected in February and August (Table 6).

The minimum size at maturity of 40 mm for female *C.n.* compares favorably with the 37 mm minimum found by Isreal (1936). For female *C.f.,* however, the 48 mm size at maturity is noticeably smaller than the 53 mm minimum reported for San Francisco Bay (Isreal, 1936). Because size at maturity is temperature dependent (Meredith, 1952), the temperatures of San Francisco Bay waters seem closer to the optimum for *C.n.* while those in Yaquina Bay seem closer to the optimum for *C.f.* A comparison of mature males was not possible because Isreal (1936) did not examine the testes of the shrimp he observed.

Various authors report extended spawning season in crangonids. Lloyd and Yonge (1947) and Meredith (1952) saw ovigerous females 10 months of the year, and Havinga (1930, cited in Lloyd and Yonge, 1947) and Price (1962) saw ovigerous females 11 months of the year. Such extended spawning seasons were normally followed by a 1- to 2-month nonreproductive period (Giese, 1959); Isreal (1936), however, found ovigerous females during all months of the year. He concluded that in San Francisco Bay there is a single but extended spawning season with the main breeding period being March-September. Meredith (1952) believed that breeding was continuous after maturity was reached and was probably controlled by the influence of temperature on the speed of development. Because the spawning season for *C.n.* in Yaquina Bay is from December to mid-August, followed by a 3½-month nonreproductive period, it is probable that the variations between lengths of spawning seasons in California and Oregon are due to the cooler Oregon climate.

The two basic spawning peaks for *C.n.* in Yaquina Bay were similar in composition and timing to that followed by *C. vulgaris* (Lloyd and Yonge, 1947; Meredith, 1952), *C. septemspinosa* (Price, 1962), and *C. allmani* (Allen, 1960). Meredith (1952) noted that females which spawned a second time did so only in the early summer. The composition and cycle of the spawning sequence was not recorded by Isreal (1936), but he did feel that some females might spawn a second time.

The "disappearance" of ovigerous females toward the end of the spawning period probably is due to a combination of the previously discussed spawning migration from the bay and mortality of large females. Meredith (1952) felt that the disappearance of large females (70-80 mm) in the summer was due to mortality and that the apparent reappearance in August and September was due to growth of shrimp from 50-60 mm to 70 mm size. Allen (1960) agreed and also felt that males die before females, probably soon after copulation. With the shrimp in Yaquina Bay, the appearance of some large individuals (>50 mm TL) in November and December and the estimated adult growth rate (Fig. 6) indicate that a few individuals survive to spawn a second time.

Both species exhibit a shorter incubation period for group II than for group I segments of the population which is likely temperature dependent. Studies on comparable species of crangonids indicate similar variations in length of incubation (Havinga, 1930, cited in Allen, 1960; Meredith, 1952; Allen, 1960).

An additional variable which could shorten the summer incubation period is salinity. Broekema (1941, cited in Allen, 1960) noted that low salinity retards egg development, with incubation requiring twice as long at 16 ppt than at 35 ppt.

All species of cragonids (Lloyd and Yonge, 1947; Meredith, 1952; Allen, 1960; Price, 1962) exhibit a differential growth rate between large females and males. The size at which the females increased their growth rate appears to be a function of the age at maturity for a particular population. *C.n.* and *C.f.* in both San Francisco Bay (Isreal, 1936) and Yaquina Bay exhibit differential growth at an early age (4-5 months after they leave the plankton).

The sex ratio of crangonid populations varied greatly from sample to sample, but averaged in favor of the females (Lloyd and Yonge, 1947; Meredith, 1952; Price, 1962). This circumstance must be due to the early death of males and to some females that live to spawn a second time. Isreal (1936) reported an imbalance of the sex ratio for *C.f.* in favor of females during breeding season and in favor of males prior to breeding season. In a pattern comparable to *C. vulgaris* and *C. allmani* (Allen 1966), the shrimp of Yaquina Bay kept a close male:female ratio prior to and during the breeding season. This type of close sex ratio is what one would expect from shrimp which lay more than one brood and exhibit nonsynchronous spawning.

Acknowledgements

We wish to thank the School of Oceanography for the use of the R/V PAIUTE and to thank Messrs. Dean Satterlee and William Johnson for their assistance during this sampling program. Our thanks also to Drs. W. G. Pearcy and C. E. Bond for review of the manuscript. This work is a result of research sponsored (in part) by the Oregon State University Sea Grant College Program. The U.S. Government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation that may appear hereon.

Literature Cited

Allen, J. A. 1960. On the biology of *Crangon allmani* Kinahan in Northumberland waters. J. Mar. Biol. Assn. U.K. 39: 481-508.

Allen, J. A. 1966. The dynamics and interrelationships of mixed populations of Caridea found off the north-east coast of England. Pages 45-66 *in* Harold Barnes, ed. Some contemporary

studies in marine science. George Allen and Unwin Ltd., London.
Bonnot, P. 1932. The California shrimp industry. Calif. Div. Fish and Game, Fish Bull. No. 38. 20 p.
Broekema, M. M. M. 1941. Seasonal movements and the osmotic behavior of the shrimp *Crangon crangon*. Acad. Thesis, Gronigen. 100 p.
Daiber, F. C. 1959. Tidal marsh. Estuarine Bull. 4(4): 4-16.
Darlington, C. D., and L. F. LaCour. 1969. The handling of chromosomes. George Allen and Unwin Ltd., London. 272 p.
Draper, N. R., and H. Smith. 1966. Applied regression analysis. John Wiley and Sons, Inc., New York. 407 p.
Ehrenbaum, E. 1890. Zur Naturgeschichre von *Crangon vulgaris* Fabr. Mitt. Sekt. Küsten-u. Hochseefisch. 24 p.
Giese, A. C. 1959. Comparative physiology: annual reproductive cycles of marine invertebrates. Annu. Rev. Physiol. 21: 547-576.
Haertel, L., and C. Osterberg. 1966. Ecology of zooplankton, benthos and fishes in the Columbia River estuary. Ecology 48(3): 459-472.
Havinga, B. 1930. Der Granat (*Crangon vulgaris* Fabr.) in den holländischen Gewässern. J. Conseil Inter. Exp. Mer. 5: 53-87.
Herdman, W. A. 1904. An outline of the shrimp question. Proc. Trans. Liverpool Biol. Soc. 18: 157-167.
Hess, P. W. 1961. Food habits of two Dasyatid rays in Delaware Bay. Copeia 2: 239-241.
Holthuis, L. B. 1951. Proposed use of the plenary powers to validate the generic name *"Crangon"* Fabricius, 1798, for the common shrimp and the generic name *"Alpheus"* Fabricius, 1798, for the snapping shrimps (Class Crustacea Order Decapoda). Bull. Zool. Nomenc. 2: 69-72.
Isreal, H. R. 1936. A contribution toward the life histories of two California shrimps, *Crago franciscorum* (Stimpson) and *Crago nigricauda* (Stimpson). Calif. Div. Fish. and Game, Fish Bull. No. 46. 28 p.
Krygier, E. E. 1974. Distribution and reproductive biology of *Crangon franciscorum* (Stimpson) and *Crangon nigricauda* (Stimson), in Yaquina Bay, Oregon. M.S. Thesis. Oregon State Univ., Corvallis, Oregon. 76 p.
Kume, M., and K. Dan. 1957. Invertebrate embryology. (Transl. from Japanese.) NSF Grant G-8663. 605 p.
Lebour, M. V. 1931. The larvae of the Plymouth Caridea. I. The larvae of the Crangonidae. II. The larvae of the Hippolytidae. Proc. Zool. Soc. London. p. 1-9.
Lloyd, A. J., and C. M. Yonge. 1947. A study of *Crangon vulgaris* in the British Channel and Severn Estuary. J. Mar. Biol. Assn. U.K. 26: 626-661.
Loveland, H. A., Jr. 1968. Larval development under laboratory conditions of *Crangon alaskensis*, Rathbun (Crustacea: Decapoda). M.S. Thesis. Walla Walla College, Walla Walla, Washington. 23 p.
Makarov, R. R. 1966. Larvae of the shrimps and crabs of the west Kamchatkan shelf and their distribution. (Transl. from Vsesoyuznoe Gidrobiologischkloie Obshch., Moskva.) Transl. Haigh, B. NLLST, Boston Spa, Yorkshire, England. 200 p.
Mendenhall, W. 1963. Introduction to probability and statistics, 2nd ed. Wadsworth Pub. Co., Inc. Belmont, Calif. 393 p.
Meredith, S. S. 1952. A study of *Crangon vulgaris* in Liverpool Bay area. Proc. Trans. Liverpool Biol. Soc. 1950-1952: 75-109.
Needler, A. B. 1941. Larval stages of *Crago septemspinosus* Say. Trans. Roy. Canad. Inst. 50: 193-199.
Price, K. S., Jr. 1962. Biology of the sand shrimp, *Crangon septemspinosa,* in the shore zone of the Delaware Bay region. Chesapeake Sci. 3(4): 244-255.
Rathbun, M. J. 1904. Decapod crustaceans of the northwest coast of North America. Harriman Alaska Exped. 10: 1-190.
Richardson, H. 1905. Monograph on the isopods of North America. U.S. Nat. Mus. Bull. No. 54. 727 p.
Rudy, Paul (Session Ldr). 1970. Some problems of the coastal zone. Pp. 119-189 *in* J. D. Findlay (Chrmn), and T. S. Roberts (Asst Chrmn). Proc. Northwest Estuarine and Coastal Zone Symposium. U.S. Bur. Sports Fish. Wildlife, Portland, Oregon.
Schmitt, W. L. 1921. The marine decapod crustacea of California. Univ. Calif., Publ. Zool. Vol. 23. 470 p.
Wenner, A. M. 1972. Sex ratio as a function of size in marine Crustacea. Am. Nat. 106(949): 321-350.

Received April 21, 1975.
Accepted for publication June 2, 1975.

Herbert A. Brown

Department of Biology
Western Washington State College
Bellingham, Washington 98225

Reproduction and Development of the Red-legged Frog, Rana aurora, in Northwestern Washington

Abstract

This study reports on the development of embryos and tadpoles of the red-legged frog, *Rana aurora,* in a permanent woodland pond. Egg laying began in late February or early March at water temperature of about 6.2°C. Duration of embryonic development was about 35 days, and water temperature ranged from 4.5 to 7.8°C. Tadpoles hatched in early April and measured 12.4 mm total length. Larval development required about 110 days, and water temperature ranged from 7.3 to 23.5°C. Body length at metamorphosis was 28.7 mm. Tadpole mouthparts developed slowly, and at stage 33 the complete tooth formula was 3(2,3)/4(1). Discussion of the comparative reproductive biology of Pacific Northwest *Rana* is included.

Introduction

Although there are many laboratory studies on the development of amphibian eggs and larval stages (see Salthe and Mecham, 1974), basic quantitative data describing development and growth in natural populations are meager. This study reports on the early life history of a woodland population of the red-legged frog, *Rana aurora,* from egg deposition to metamorphosis of the tadpoles. Data on timing, development and growth in embryos and tadpoles are presented. These kinds of data are essential for the analysis of environmental adaptation and comparisons of reproductive strategy (see Milstead, 1972).

Already there are a few studies on the comparative biology of the *Rana* species complex in the Pacific Northwest of the United States (Dumas, 1966; Haertel and Storm, 1970; Licht, 1969, 1971). The reproductive biology of *R. aurora* is particularly well known from studies of breeding behavior and mating call (Licht, 1969, 1971), interspecific hybridization (Porter, 1961; Dumas, 1966), embryonic adaptations to temperature (Licht, 1971), and natural mortality of embryos and tadpoles (Calef, 1973; Licht, 1974). This study contributes further information for a comparison of the reproductive ecology of Pacific Northwest frogs.

Materials and Methods

Field work was done at a permanent beaver pond in the Lake Louise Wildlife Sanctuary, about 8 km (5 mi) east of Bellingham, Whatcom County, Washington. The pond is small (about one acre) and is situated at an elevation of about 120 m (400 ft). It is surrounded by alder-evergreen woods, and a small permanent stream (Beaver Creek) leaves the pond and flows into Lake Whatcom. During summer the pond level is kept relatively stable by underground springs.

Mating behavior and oviposition were observed during three breeding seasons (1971-73). Breeding activity (determined by presence of calling males and new egg

masses) usually began in late February or early March and continued for only two or three weeks. The males called from beneath the water surface, and most egg masses were attached to stalks of grass or branches of submerged logs near the edge of the pond.

During the 1973 breeding season the field development of 35 recently laid egg masses (individually marked with numbered plastic tags) was measured by periodically sampling 10 embryos from each mass and determining their stage of development by using the staging system of Gosner (1960): cleavage (stages 3 to 9), gastrulation (st. 10 to 12), neurulation (st. 13 to 16), tailbud (st. 17), muscular response (st. 18), heart beat (st. 19), and gill circulation (st. 20). Each sample, placed in a small vial and carried in ice water, was examined with a binocular dissecting microscope about two hours after collection. Measurements of the development and growth of the free-swimming larval stages were made by collecting samples of tadpoles with a dip net, preserving them in 10 percent formalin, and later determining their stage of development (Gosner, 1960). The following measurements on the tadpoles were made in the laboratory: (1) body weight (preserved animal air-dried for one minute); (2) body length (BL), measured from tip of snout to midpoint of the cloacal region; (3) tail length (TL), measured from midpoint of cloacal region to the tip of the tail; (4) body width (BW), measured across widest part of the body; (5) tail depth (TD), measured at the greatest point along tail; (6) total length (ToL), computed by adding values of body and tail length. Notes on the development of tadpole mouthparts were made also.

During the field study the water temperature near the developing egg masses was monitored with maximum-minimum thermometers placed at depths of 30 and 75 cm. Also a Schultheis quick registering thermometer was used to measure temperature within the egg masses and the surrounding water.

Results

Embryonic Development. During the three years of observation at the beaver pond, breeding activity began between 17 February and 5 March. I heard and observed male frogs calling beneath the water where temperature ranged from 4 to 9°C. The minimum water temperature at which egg laying began was about 6°C, and this finding agrees with the observations of Licht (1971) for a coastal population in southwestern British Columbia. The egg masses are large (about 15 to 25 cm diameter), and each contains about 600 eggs. Most egg masses were found near the edge of the pond, and here I marked and studied egg masses placed between 25 and 75 cm in depth.

The pattern of embryonic development in the pond (Fig. 1) is a composite of data collected from 35 egg masses during 15 visits between 18 February and 7 April. The average time from egg deposition (stage 1) to gill circulation (st. 20) was about 35 days. My data show that the cleavage period (st. 3 to 10) required 6 to 9 days; gastrulation (st. 10 to 13) was 5 to 7 days, and organogenesis (st. 13 to 20) was 20 to 23 days. Storm (1960) studied reproduction and development of *R. aurora* in western Oregon and found that the time from laying to hatching was 35 to 49 days. Embryos of *R. sylvatica* (a close relative to *R. aurora*) have an incubation period of 4 to 7.5 days in Alaska at water temperatures of about 15 to 18°C (Herreid and Kinney, 1967); in Tennessee the incubation period is 18 to 20 days at an average water temperature of 8.3°C (Meeks and Nagel, 1973).

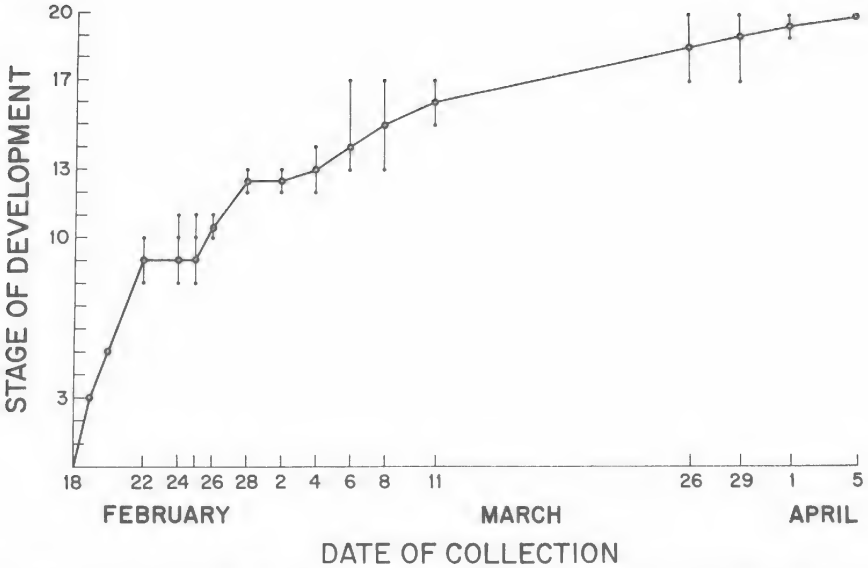


Figure 1. Embryonic development of red-legged frogs in beaver pond. Data show most common developmental stage (large symbol) and other developmental stages (small symbol) of marked egg masses observed in the pond.

Temperature is the major factor controlling the developmental rate of amphibian embryos. The water temperatures near the developing egg masses ranged from a low of 2°C to a high of 9°C. The average minimum temperature was 4.5°C and the average maximum, 7.8°C; an average water temperature of 6.2°C was estimated from the median value of maximum-minimum recordings.

Licht (1971) studied embryonic adaptations to temperature in a population of *R. aurora* in southwestern British Columbia; tolerance limits were 4 to 21°C and developmental rates (time between stages 3 and 20) were about 1350 hr at 4.5°C, 630 hr at 7°C, and 250 hr at 15°C. Compared to other cold-adapted anurans (*Hyla regilla* and *Ascaphus truei*) living in the same region, the embryos of *R. aurora* develop very rapidly at low temperatures (Brown, 1975a, b). Using the data of Licht (1971) where eggs developed at constant temperature in the laboratory, embryonic development at 6°C required about 820 hr or 34 days. Thus, there is close agreement in developmental rate of embryos developing in the pond and the laboratory. I found this relationship in treefrog embryos also (Brown, 1975b). Herreid and Kinney (1967) found no difference in developmental rate of *R. sylvatica* embryos (through stage 20) when raised in the laboratory at fluctuating or constant temperatures.

Several studies show that egg-mass temperature may be higher than the surrounding water (Savage, 1961; Herreid and Kinney, 1967; Hassinger, 1970), and temperatures in the egg masses of *R. aurora* may be 3.6°C higher than the water (Licht, 1971). During early March on clear sunny days I found that the temperature within 10 *R. aurora* egg masses averaged 8.7°C while that of the surrounding water was 7.7°C. Licht (1971) found egg masses averaging 15.3°C and water, 13.8°C.

Because of the early breeding season the egg masses of *R. aurora* may be exposed

to very low temperatures. On several occasions in late February freezing temperatures resulted in ice covering parts of the beaver pond. However the egg masses were developing at more than 10 cm from the surface, and the cold did not harm the embryos. Embryonic mortality at gill circulation (st. 20), estimated from the percentage of abnormal embryos in the 35 egg masses, was low (about 6%). Licht (1974) studied survival of embryos and tadpoles of *R. aurora* and *Rana pretiosa* sympatric in southwestern British Columbia; *R. aurora* lay eggs in deep water and have a low mortality (about 10%) while *R. pretiosa* lay eggs in shallow water and have a high mortality (about 30%).

Larval Development. Embryos hatch from the jelly capsules and generally remain near the egg mass for several days. Although they are capable of swimming they attach to the egg mass or rest on underwater plants or debris. The average total length at hatching is 12.4 mm. Storm (1960) reported that hatching size varied between 11 and 12 mm.

The pattern of larval development and growth in the pond was determined by examining tadpoles collected periodically between early April and late July. Growth curves (Fig. 2) for body weight, total length, body length, tail length, and body width quantify changes in body size as tadpoles developed in the pond. The variation in these dimensions at eight developmental stages is shown in Table 1.

Postembryonic development of anuran tadpoles can be divided into three periods (Etkin, 1968): (1) premetamorphosis (st. 25 to 38) when there is much growth but little differentiation; (2) prometamorphosis (st. 38 to 42) when growth rate slows but morphological changes accelerate; and (3) metamorphic climax (st. 42 to 46) when drastic changes in transformation of the head, appearance of the forelimbs and resorption of the tail occur. In this study, the first tadpoles (st. 21) hatched from the marked egg masses on 5 April, and the first sample showing complete metamorphosis (st. 46) was 23 July. Thus, the total time of postembryonic development was about 110 days; premetamorphosis was about 78 days, prometamorphosis about 20 days, and metamorphic climax about 12 days.

The rate of development and growth of tadpoles (Fig. 2) during the first two weeks were slow; mean body length increased gradually from stage 23 (5.1 mm) to stage 25 (6.5 mm). The average growth rate (total length) from stages 23 to 30 was 0.62 mm/day; between stages 30 and 39 growth rate was 0.99 mm/day. Calef (1973) studied growth of *R. aurora* tadpoles in a natural population inhabiting a shallow lake in southwestern British Columbia; during the first month of larval development body length increased from about 6 mm to about 12 mm (similar to my data), but during the following two months growth was slow (contrary to my data). The rapid growth of tadpoles during June produced the largest and heaviest tadpoles at stages 39 and 40; the average maximum size was 6.46 g and 75.9 mm total length.

Since free-swimming tadpoles may select preferred temperatures from a wide spectrum available in the pond, the data of pond temperatures from the maximum-minimum thermometers can only indicate the general trend of increasing pond temperatures. During April the median temperature was 10°C (mean maximum of 12.3°C and mean minimum of 7.3°C). During May these values were 12.2°C (18.2 and 9.3°C); during June, 20.3°C (23.2 and 14.3°C); during July, 20.7°C (23.5 and 15.5°C). The low temperatures of April and May in part account for the slow tadpole

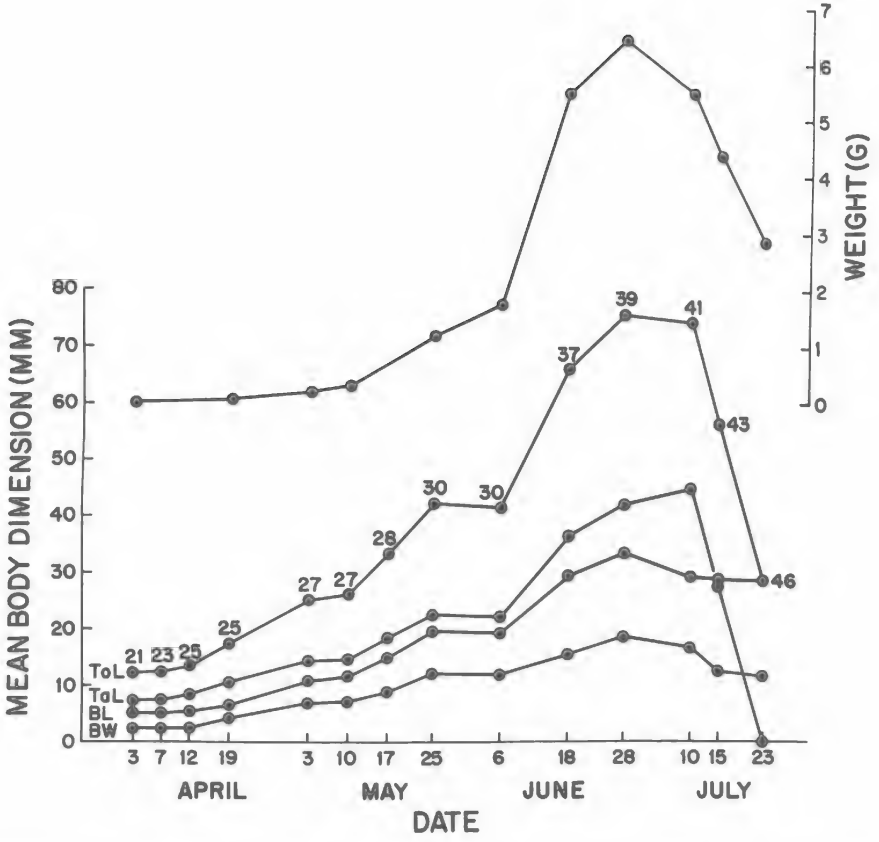


Figure 2. Development and growth of red-legged frog tadpoles in beaver pond. The upper line in the figure represents weight change; the lower four lines show change in total length (ToL), tail length (TaL), body length (BL), and body width (BW). The stages of tadpole development are indicated at the points of the growth curve for total length.

growth between stages 23 and 30, and the higher temperatures of June and July, for the rapid growth between stages 30 and 39.

The long period of larval growth in *R. aurora* permitted the development of large-sized tadpoles at metamorphosis. Although average body length at stage 39 was 33.7 mm, body length at the completion of metamorphosis was 28.7 mm. Storm (1960) reported that body length in recently metamorphosed *R. aurora* from a temporary pool ranged from 20 to 25 mm; Calef (1973) reported a value of about 22 mm.

Limbaugh and Volpe (1957) reported that relative body ratios during larval development of frogs may be relatively constant and useful in taxonomic studies. Thus, the five body dimensions measured in this study are also expressed in terms of ratios (Table 1). The ratios of body length to total length (BL/ToL) and tail length to total length (TaL/ToL) remained relatively constant (0.43 and 0.57, respectively).

TABLE 1. Growth and development of tadpoles of *R. aurora*. Linear measurements in millimeters. Data show mean ± standard deviation and range; 25 tadpoles in each sample.

Date	Stage	Body length	Tail length	Total length	Body width	Tail Depth	BL/ToL	TaL/ToL	BW/TD
4/3/73	23	5.1±0.4 4.4 – 7.0	7.3±0.3 5.9 – 7.9	12.4±0.3 11.6 – 12.9	2.3±0.1 2.0 – 2.7	3.2±0.2 2.9 – 3.6	0.41±0.05 0.37 – 0.54	0.59±0.01 0.41 – 0.62	0.71±0.03 0.64 – 0.75
5/3/73	27	10.9±0.5 9.8 – 12.3	14.2±0.4 12.0 – 16.6	25.1±0.9 21.8 – 28.5	6.9±0.3 6.0 – 8.0	8.0±0.4 6.6 – 9.0	0.43±0.02 0.38 – 0.46	0.57±0.02 0.54 – 0.62	0.84±0.02 0.82 – 0.97
5/25/73	30	19.5±0.9 17.0 – 24.0	22.6±0.8 20.4 – 25.7	42.1±1.7 37.4 – 49.7	12.1±0.5 11.1 – 15.0	13.0±0.8 11.1 – 15.2	0.46±0.01 0.44 – 0.48	0.54±0.02 0.52 – 0.56	0.84±0.02 0.86 – 1.01
6/18/73	37	29.7±0.5 28.5 – 31.7	36.5±1.1 34.5 – 40.3	66.2±2.7 62.7 – 70.5	15.5±0.7 14.8 – 15.9	15.7±0.6 14.9 – 16.1	0.45±0.03 0.41 – 0.47	0.55±0.02 0.52 – 0.58	0.99±0.04 0.91 – 1.07
6/28/73	39	33.7±0.4 33.2 – 35.5	42.1±2.7 36.2 – 48.9	75.9±2.4 69.0 – 82.1	19.8±0.8 17.7 – 21.2	18.3±0.7 16.0 – 19.5	0.45±0.02 0.40 – 0.48	0.55±0.02 0.52 – 0.58	1.08±0.05 1.02 – 1.20
7/15-73	43	28.9±0.6 27.3 – 30.9	27.3±4.7 12.3 – 38.1	56.3±4.6 40.8 – 68.2	12.4±0.6 11.3 – 13.5	8.6±1.7 4.5 – 11.5	0.54±0.07 0.42 – 0.70	0.46±0.09 0.30 – 0.58	1.58±0.11 1.04 – 1.98
7/20/73	44	28.6±0.6 27.3 – 29.7	2.2±1.1 0.3 – 3.4	30.7±0.5 29.9 – 31.5	12.0±0.3 11.4 – 12.6	2.4±0.2 2.1 – 2.7	0.93±0.02 0.89 – 0.99	0.07±0.02 0.01 – 0.11	5.03±2.3 4.62 – 5.86
7/23/73	46	28.7±0.7 27.4 – 29.6	0.0±0.0 0.0 – 0.0	28.7±0.7 27.4 – 29.6	11.7±0.2 10.7 – 12.7	0.0±0.0 0.0 – 0.0	1.00±0.00 1.00 – 1.00	0.00±0.00 0.00 – 0.00	0.00±0.00 0.00 – 0.00

The ratio of body width to tail depth (BW/TD) showed a gradual increase from 0.71 at stage 23 to 1.08 at stage 39. Haertel and Storm (1970) found that the ratio of body width to tail depth was relatively constant from stages 26 to 41 for *Rana pretiosa* (0.92) and *Rana cascadae* (1.18), and that this ratio in hybrid tadpoles (*R. cascadae* X *R. pretiosa*) was intermediate (about 1.02). This ratio for *R. aurora* tadpoles is intermediate also.

The larval mouthparts of *R. aurora* show the basic ranid pattern (see Altig, 1970). The papillary border is incomplete on the anterior lip and shows an indentation at the corners of the mouth. There is a single row of papillae anteriorly and posteriorly, but there are several rows laterally. The mouthparts achieve complete development at stage 33, and the maximum tooth row formula is 3(2,3)/4(1). There are three rows of teeth on the upper labium and four rows on the lower labium. The first upper row is complete; the second and third rows (near the corner of the mouth) are small and lack the medial portion. In the lower labium the first row has a small, median gap (almost absent), but the other three rows are complete; the second row is slightly shorter than the first row, and the third slightly shorter than the second; the fourth row is the shortest, being about equal to 50 percent of the first lower row.

The larval mouthparts of *R. aurora* develop slowly. On 5 April the first tadpoles hatched at stage 21. However, on 19 April a sample of tadpoles at stage 25 showed the development of the horny beak, but there were no labial teeth and the adhesive organ (oral suckers) was still present. On 26 April tadpoles at stage 26 had developed labial teeth (formula 1/2 and 1/3), but the adhesive organ was still evident. On 3 May at stage 27 the formula was 1/3, and there were vestiges of the adhesive organ. On 10 and 17 May at stage 27 the formula was 2/3, and the adhesive organ was absent. On 25 May and 6 June at stage 30 the formula was 2/4. On 12 June at stage 33 the formula was 3/4 (sometimes 3/3); in some tadpoles the third lower row was divided, and one side continued posterior to the other side as the fourth row, and this condition made the tooth formula 3/4 on one side but 3/3 on the other.

These differences in tooth formula illustrate developmental and individual variation (Hampton and Volpe, 1963) and emphasize the need for designating the tooth formula at a specific developmental stage and the necessity of studying many specimens at a given stage. Stebbins (1966) reported that *R. aurora* has a tooth formula of 2/3, and Altig (1970) described two conditions, 3/3 and 3/4. Haertel and Storm (1970) found that the larval mouthparts of *R. pretiosa* (tooth formula, 2(2)/3(1)) are fully differentiated by stage 28, but in *R. cascadae* (tooth formula, 3(2,3)/4) the mouthparts are completed at stage 33. Thus, the population of *R. aurora* in my study is similar to *R. cascadae*: tooth formula is 3/4 and mouthparts develop slowly.

Discussion

Studies on reproduction and development of amphibians have provided much evidence for comparing the reproductive strategy of different species (see Worthington, 1968; Licht, 1969, 1971; Hassinger *et al.*, 1970) or different populations of the same species (see Pettus and Angleton, 1967; Brown, 1975b). There is considerable data showing that developmental rate and growth are susceptible to modification by environmental factors (see Salthe and Mecham, 1974). Nevertheless, detailed field studies on development and growth of eggs and tadpoles have been limited to a few species:

Scaphiopus bombifrons (Voss, 1961), *Rana sylvatica* (Herreid and Kinney, 1967; Meeks and Nagel, 1973), *Rana septentrionalis* (Hedeen, 1971), and *Rana pretiosa* (Morris and Tanner, 1969).

The reproductive biology of many frogs (*Rana*) in western North America is still only partially known. Comparative studies of osteology (see Chantell, 1970), ecology (Zweifel, 1955), karyotypes (Haertel *et al.,* 1974), and blood proteins (Wallace *et al.,* 1973) suggest two closely related groups: (1) *boylei* and *muscosa,* and (2) *aurora, sylvatica, pretiosa,* and *cascadae.* The former group seems closely related to Mexican *Rana* (Zweifel, 1955) and the latter to Palearctic *Rana* (Wallace *et al.,* 1973). Zweifel (1955) provides some information on the development of eggs and tadpoles of the *boylei-muscosa* group.

Dumas (1966) studied the evolutionary and biogeographical relationships of the Pacific Northwest *Rana* and suggested two groups based upon their general natural history: the early-breeding (January-April) wood frogs, *aurora* and *sylvatica,* and the late-breeding (March-early July) pond frogs, *pretiosa* and *cascadae.* These frogs are ecologically distinct and basically allopatric. In the Pacific Northwest *aurora* is found at low elevations west of the Cascade Mountains; *cascadae* inhabits the higher montane regions of the Cascades; *pretiosa* is found chiefly at low elevations east of the Cascades, but there are isolated populations west of the Cacades (Dumas, 1966); *sylvatica* is a northern species found from Alaska through Canada to the northeastern United States, and the nearest populations in the Pacific Northwest occur in northern Idaho and central British Columbia (Stebbins, 1966).

Licht (1971) studied the embryonic adaptations to temperature in *aurora* and *pretiosa* and compared them to *sylvatica* and other eastern *Rana.* Embryos of *aurora* have the lowest limiting temperatures (4 and 21°C) but the slowest developmental rate, whereas *sylvatica* has higher temperature limits (6 and 24°C) and the fastest rate of development; *pretiosa* has a broad temperature limit (6 and 28°C) and intermediate developmental rates.

There is some information on the embryonic temperature adaptations of *cascadae.* Porter (1961) suggested that "although the Cascade frog is found at higher elevations, its embryonic development is undoubtedly adapted to warmer temperatures than that of the lowland form [*aurora*]." He reported that *cascadae* breeds from late May to July, deposits eggs in shallow ponds or shallow portions of deep pools, and that the optimum temperature for embryonic development is about 19.9°C. I found a population of *cascadae* breeding 12 May 1973 in shallow pools near Boardman Lake (3500 ft, 1060 m), Snohomish County, Washington; egg masses with embryos at the 4-cell, gastrula, neurula and tail-bud stages were developing in water where temperature ranged from 16.8 to 31.3°C, with an average of 23.3°C (Brown, unpublished). Since Dumas (1966) found normal development at 11°C, the embryonic temperature limits of *cascadae* appear to be similar to those of *pretiosa* and may range from 6 to 30°C. The few observations of reproduction of *cascadae* and *pretiosa* suggest adaptations to temporary waters (roadside ditches, shallow pools in grassy meadows, and the shallow margins of small lakes or streams). In the short growing season of the montane environment, shallow, temporary pools provide warm conditions that hasten development of eggs and tadpoles of *cascadae.*

Accurate information on water temperatures and duration of embryonic develop-

ment of Pacific Northwest *Rana* is meager, but such data are required for the interpretation of comparative studies on temperature tolerance and developmental rate (see Morris and Tanner, 1969). We need more information on developmental ecology of these frogs; this should include comparative studies of geographic variation and habitats utilized (permanent or temporary waters).

Morris and Tanner (1969) studied reproductive ecology of *pretiosa* in Utah, and they reported: (1) *pretiosa* began egg laying in middle or late March when water temperature was about 14°C; *aurora* (this study) required 6°C; (2) *pretiosa* eggs developed rapidly in about 14 days; *aurora* eggs (this study) required about 35 days; (3) average water temperature during development of *pretiosa* eggs was about 16°C; *aurora* eggs (this study) developed in water of about 6.2°C; (4) *pretiosa* tadpoles hatched with a total length of 8-10 mm; Svihla (1935) reported that eastern Washington *pretiosa* hatched with a length of 7.3-8.7 mm; *aurora* tadpoles (this study) hatched with a length of 12.4 mm; Storer (1925) reported that California *aurora* hatched with a length of 8.8-10.3 mm. There is almost no information on embryonic development of *cascadae,* but Slater (1939) reported that eggs hatch after incubation of 8 to 20 days.

Information on larval development is scanty also. Morris and Tanner (1969) reported: (1) *pretiosa* tadpole growth between stages 26 and 37 was rapid (1.5 to 2.7 mm/day), and maximum total length was about 64 mm; growth rate of *aurora* tadpoles (this study) was slow (0.62 to 0.99 mm/day), and maximum length was 75.9 mm; (2) *pretiosa* larval development required about 108 days, and metamorphosis began in late July when body length was about 28 mm; Svihla (1935) reported that *pretiosa* tadpoles of eastern Washington developed rapidly, and metamorphosis began in mid-June at a body length of about 26 mm; *aurora* tadpoles (this study) required about 110 days, and body length at metamorphosis was 28.7 mm; Storer (1925) reported that California *aurora* tadpoles required 5 to 7 months, and body length at metamorphosis was 18-30 mm. Slater (1939) reported that development of *cascadae* tadpoles required 80 to 95 days, and body length at metamorphosis was 14 mm or less; however, Wright and Wright (1949) measured other specimens, described as "just transformed," with a body length of 21-23 mm. These observations suggest *pretiosa* and *cascadae* have faster rates of embryonic and larval development than does *aurora,* and that *aurora* tadpoles have a larger body size at metamorphosis than do *pretiosa* and *cascadae.*

Reproduction in populations of *cascadae* and *pretiosa* frequently occurs in shallow, temporary pools. During the hot, dry summer of the montane zone (*cascadae*) and the arid transition zone (*pretiosa*) selection favors rapid development in such pools. In contrast, reproduction in *aurora* usually occurs in permanent pools (sometimes temporary waters) in the humid transition zone. The slow development rate of *aurora* tadpoles may result from several factors: (1) selection pressures for rapid development may be low because of the moderate temperature conditions or absence of interspecific competition for food from other species of ranid tadpoles; and (2) there may be selection for slow rate of development since this correlates with large size at metamorphosis. The large size is adaptive because there is a favorable physiological advantage in water conservation as volume increases; during dry summer periods the larger frog will have a greater chance of survival than do smaller frogs (see Claussen, 1969). These relationships agree with the suggestion of Zweifel (1968) that "species with rapid rates of embryonic development have rapid rates of larval development, and

these in turn correlate with the permanency of the water supply of the breeding site."

Wiens (1970, 1972) reported that *cascadae* and *aurora* tadpoles select different artificial substrate patterns; *aurora* select striped patterns and *cascadae* select the reverse. Field observations on the developmental ecology of these frogs partially substantiated the laboratory studies.

Tadpole mouthparts (jaws, labial teeth, and papillae) presumably assist in food collection. There are many studies now on feeding mechanisms (Kenny, 1969; Wassersug, 1972), food habits (Jenssen, 1967; Dickman, 1968), anatomy of the gut (Altig and Kelly, 1974), and digestive enzymes (Altig *et al.,* 1975). The significance of the slow development of mouthparts in *aurora* tadpoles is not known. There is a need for further studies on the ontogeny of larval mouthparts and feeding habits of *aurora, cascadae,* and *pretiosa* tadpoles.

Sufficient biological information has not accumulated to permit extensive comparison of the reproductive strategies of Pacific Northwest *Rana.* We still need basic information on the reproductive behavior of adults, developmental temperature adaptations, and patterns of larval development. However, this study provides some insight concerning the reproductive strategy of *aurora.* The red-legged frog pattern of early breeding, relatively rapid embryonic development at low temperatures, and protracted larval development resulting in large size at metamorphosis is adaptive to breeding in permanent cool waters in the Pacific Northwest.

Summary

The red-legged frog (*R. aurora*) in northwestern Washington breeds for two or three weeks in late February or early March. The duration of embryonic development was about 35 days, and water temperature ranged from 4.5 to 7.8°C (mean of 6.2°C). Tadpoles hatched in early April and measured 12.4 mm total length. Larval growth was relatively constant (0.62 to 0.99 mm/day), and tadpoles reached maximum size at stage 39 (6.46 g and 75.9 mm total length). During larval development, water temperature ranged from 7.3 to 23.5°C (mean of about 16°C). Larval development required about 110 days, and tadpoles metamorphosed in late July at a body length of 28.7 mm. The tadpole mouthparts developed slowly, and at stage 33 the complete tooth formula was 3(2,3)/4(1). This pattern of early breeding, relatively rapid embryonic development at low temperatures, and protracted larval development resulting in large size at metamorphosis is adaptive to breeding in permanent cool ponds in the Pacific Northwest.

Literature Cited

Altig, R. 1970. A key to the tadpoles of the continental United States and Canada. Herpetologica 26(2): 180-207.

————, and J. P. Kelly. 1974. Indices of feeding in anuran tadpoles as indicated by gut characteristics. Herpetologica 30(2): 200-203.

————, ————, M. Wells, and J. Phillips. 1975. Digestive enzymes of seven species of anuran tadpoles. Herpetologica 31(1): 104-108.

Brown, H. A. 1975a. Temperature and development of the tailed frog, *Ascaphus truei.* Comp. Biochem. Physiol. 50(2A): 397-405.

————. 1975b. Embryonic temperature adaptations of the Pacific treefrog, *Hyla regilla.* Comp. Biochem. Physiol. 51A: 863-873.

Calef, G. W. 1973. Natural mortality of tadpoles in a population of *Rana aurora.* Ecology 54(4): 741-758.

Chantell, C. J. 1970. Upper Pliocene frogs from Idaho. Copeia 1970 (4): 654-664.

Claussen, D. L. 1969. Studies on water loss and rehydration in anurans. Physiol. Zool. 42: 1-14.

Dickman, M. 1968. The effect of grazing by tadpoles on the structure of a periphyton community. Ecology 49: 1188-1190.
Dumas, P. C. 1966. Studies of the *Rana* species complex in the Pacific Northwest. Copeia 1966(1): 60-74.
Etkin, W. 1968. Hormonal control of amphibian metamorphosis. *In* Metamorphosis (Eds. W. Etkin and L. I. Gilbert), pp. 313-348. Appleton-Century-Crofts, New York.
Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16: 183-190.
Haertel, J. D., A. Owczarzak, and R. M. Storm. 1974. A comparative study of the chromosomes from five species of the genus *Rana* (Amphibia: Salientia). Copeia 1974(1): 109-114.
———, and R. M. Storm. 1970. Experimental hybridization between *Rana pretiosa* and *Rana cascadae*. Herpetologica 26(4): 436-446.
Hampton, S. H., and E. P. Volpe. 1963. Development and intrapopulation variability of the mouthparts of *Scaphiopus holbrooki*. Amer. Midland. Natur. 70: 319-328.
Hassinger, D. D. 1970. Notes on the thermal properties of frog eggs. Herpetologica 26(1): 49-51.
———, J. D. Anderson, and G. H. Dalrymple. 1970. The early life history and ecology of *Ambystoma tigrinum* and *Ambystoma opacum* in New Jersey. Amer. Midland. Natur. 84: 474-495.
Hedeen, S. E. 1971. Growth of the tadpoles of the Mink frog, *Rana septentrionalis*. Herpetologica 27(2): 160-165.
Herreid, C. F., and S. Kinney. 1967. Temperature and development of the wood frog, *Rana sylvatica*, in Alaska. Ecology 48: 579-590.
Jenssen, T. A. 1967. Food habits of the green frog, *Rana clamitans*, before and during metamorphosis. Copeia 1967(2): 214-218.
Kenny, J. S. 1969. Feeding mechanisms in anuran larvae. J. Zool. (London), 157: 225-246.
Licht, L. E. 1969. Comparative breeding behavior of the red-legged frog (*Rana aurora aurora*) and the western spotted frog (*Rana pretiosa pretiosa*) in southwestern British Columbia. Can. J. Zool. 47(6): 1287-1299.
———. 1971. Breeding habits and embryonic thermal requirements of the frogs, *Rana aurora aurora* and *Rana pretiosa pretiosa*, in the Pacific Northwest. Ecology 52(1): 116-124.
———. 1974. Survival of embryos, tadpoles, and adults of the frogs *Rana aurora aurora* and *Rana pretiosa pretiosa* sympatric in southwestern British Columbia. Can. J. Zool. 52(5): 613-627.
Limbaugh, B. A., and E. P. Volpe. 1957. Early development of the Gulf Coast toad, *Bufo valliceps* Weigmann. Amer. Mus. Novitates (1842): 1-32.
Meeks, D. E., and J. W. Nagel. 1973. Reproduction and development of the wood frog, *Rana sylvatica*, in eastern Tennessee. Herpetologica 29(2): 188-191.
Milstead, W. W. 1972. Toward a quantification of the ecological niche. Amer. Midland. Natur. 87: 346-354.
Morris, R. L., and W. W. Tanner. 1969. The ecology of the western spotted frog, *Rana pretiosa pretiosa* Baird and Girard, a life history study. Great Basin Natur. 29: 45-81.
Pettus, D., and G. M. Angleton. 1967. Comparative reproductive biology of montane and piedmont chorus frogs. Evolution 21(3): 500-507.
Porter, K. R. 1961. Experimental crosses between *Rana aurora aurora* and *Rana cascadae*. Herpetologica 17(3): 156-165.
Salthe, S. N., and J. S. Mecham. 1974. Reproductive and courtship patterns. *In* Physiology of the Amphibia (Edited by B. Lofts) Vol. II, pp. 309-521. Academic Press, New York.
Savage, R. M. 1961. The Ecology and Life History of the Common Frog, *Rana temporaria temporaria*. Hafner Publishing Co., New York.
Slater, J. R. 1939. Description and life-history of a new *Rana* from Washington. Herpetologica 1: 145-149.
Stebbins, R. C. 1966. A Field Guide to the Western Reptiles and Amphibians. Houghton-Mifflin, Boston, Mass.
Storer, T. I. 1925. A synopsis of the Amphibia of California. Univ. California Publ. Zool. 27: 1-342.
Storm, R. M. 1960. Notes on the breeding biology of the red-legged frog (*Rana aurora aurora*). Herpetologica 16: 251-259.
Svihla, A. 1935. Notes on the western spotted frog, *Rana pretiosa pretiosa*. Copeia 1935(3): 119-122.
Voss, W. J. 1961. Rate of larval development and metamorphosis of the spadefoot toad, *Scaphiopus bombifrons*. Southwestern Natur. 6: 168-174.
Wallace, D. G., M. King, and A. C. Wilson. 1973. Albumin differences among ranid frogs: taxonomic and phylogenetic implications. Syst. Zool. 22: 1-13.
Wassersug, R. 1972. The mechanism of ultraplanktonic entrapment in anuran larvae. J. Morphol. 137: 279-288.
Wiens, J. A. 1970. Effects of early experience on substrate pattern selection in *Rana aurora* tadpoles. Copeia 1970(3): 543-548.
———. 1972. Anuran habitat selection: early experience and substrate selection in *Rana cascadae* tadpoles. Anim. Behav. 20: 218-220.

Worthington, R. D. 1968. Observations on the relative sizes of three species of salamander larvae in a Maryland pond. Herpetologica 24: 242-246.
Wright, A. H., and A. A. Wright. 1949. Handbook of Frogs and Toads of the United States and Canada. Comstock Publ. Co., Ithaca, New York.
Zweifel, R. G. 1955. Ecology, distribution, and systematics of frogs of the *Rana boylei* group. Univ. California Publ. Zool. 54 (4): 207-292.
————. 1968. Reproductive biology of anurans of the arid Southwest, with emphasis on adaptation of embryos to temperature. Bull. Amer. Mus. Nat. Hist. 140: 1-64.

Received February 14, 1975.
Accepted for publication July 7, 1975.

J. D. Hedlund
D. T. McCullugh
and
W. H. Rickard

Ecosystems Department
Battelle Memorial Institute
Pacific Northwest Laboratories
Richland, Washington 99352

Mouse Populations on Knob and Kettle Topography in South-Central Washington[1]

Abstract

A live-trap, mark and recapture study was conducted over a one-year period in unusual knob and kettle topography located adjacent to the operating N-reactor and steam electric facilities on the Hanford Reservation, Benton County, Washington. The sparse population of small mammals observed is believed to be a reflection of stony soil rather than the effects of construction and operation of the nuclear facility.

Introduction

Mouse populations have been studied in the steppe regions of south-central Washington to investigate the effect of increasing altitude and associated vegetation changes upon their distribution and bioenergetics, and population dynamics (Kritzman, 1974; Schreiber, 1973; O'Farrell *et al.,* 1972, 1974).

This study reports the results of a year-long trap study of mice in unusual knob and kettle topography in the arid shrub-steppe region of south-central Washington where A.E.C. plutonium production facilities have been in operation since 1945, and adjacent to the nuclear power plant facility with the longest operating history of the state of Washington.

The Site

The study site is located on the south bank of the Columbia River in Benton County, Washington, Township 14N, Range 26E, Section 27, near the operating N-reactor (Fig. 1). The soil consists of fine-textured material mixed with river-washed gravel, cobbles, and boulders.

The climatic conditions are representative of the shrub-steppe region in south-central Washington. Average annual precipitation as measured at the Hanford meteorological station is slightly less than 7 inches, occurring mostly in fall and winter. The summer months are characteristically very hot and dry.

The vegetational cover consists largely of Sandberg bluegrass, *Poa sandbergii,* and cheatgrass, *Bromus tectorum* (Fig. 2). Sagebrush, *Artemisia tridentata,* is lacking because of a fire history (Rickard, 1974).

[1] This paper is based upon work performed for United Engineers and Constructors, Inc., Philadelphia, PA.

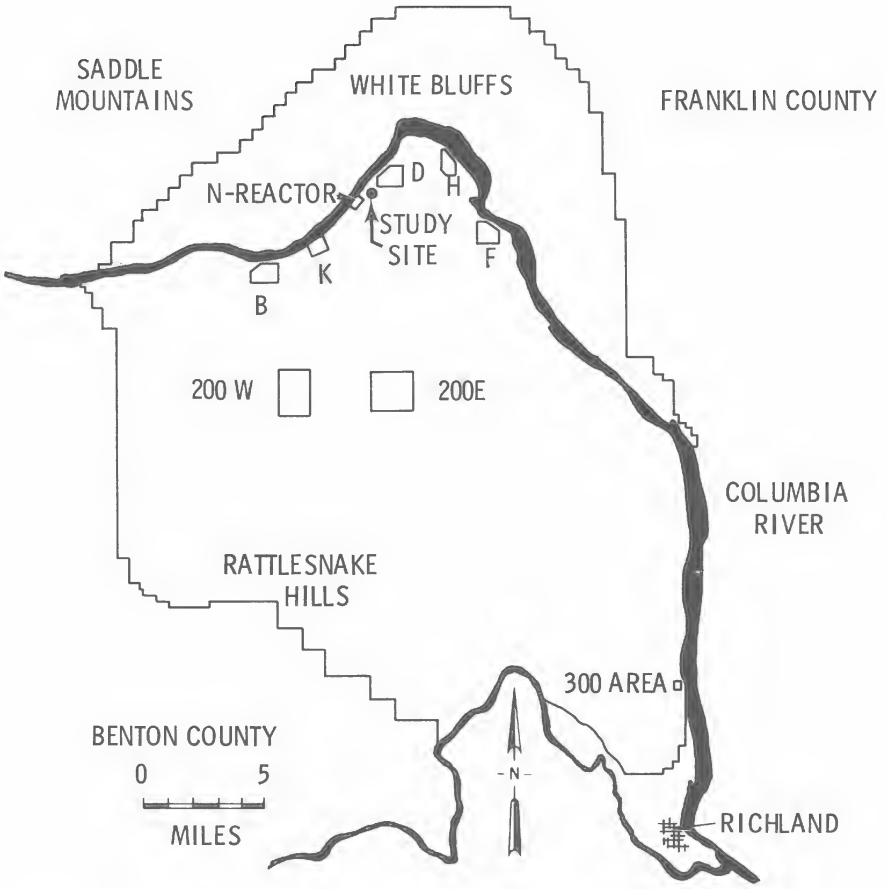


Figure 1. The location of the study area on the Hanford Reservation, Benton County, Washington.

Methods Employed

The 2.7-hectare study area included broad ridges and shallow swales. A 12 x 12 trapping grid (144 stations) at 15-meter intervals was surveyed, and one Sherman live trap placed at each station. The traps were placed inside metal cans, and these, in turn, were covered with galvanized steel tents to provide insulation from environmental extremes of heat, cold, wind, and precipitation. Each trap contained dacron batting material for insulation and a sufficient quantity of mixed seeds to prevent the trapped animals from becoming torpid during confinement.

The traps were opened in the midafternoon and were baited with a small quantity of an oatmeal-peanut butter mixture. The following morning the traps were checked and the trapped animals removed and examined. Each animal was marked with toe amputations to identify individuals. Trap station, species, sex, reproductive condition, age, and weight were recorded, and the animal released. Weighing was done in the field using a calibrated spring scale.

Figure 2. Ground-level photograph of knob and kettle topography.

The data were transcribed onto computer data sheets for storage and retrieval. A computer routine which summarized all previous captures and locations of individuals was used to facilitate identification of the toe-clip marks in the field during the next trapping session.

Trapping sessions were conducted monthly during the spring and summer when the animals were most active and bimonthly during winter when mice were mostly inactive. Each trapping session consisted of three or four consecutive nights, depending on the numbers of new animals captured on the second and third days, an indicator of trapping efficiency. Areas of activity were arbitrarily sketched on a map representing the trap grid system, but always based upon at least four captures.

To provide an objective way to estimate the depth of soil over rocks, a metal rod 1/4″ in diameter was pushed into the soil until it met a solid resistance. One hundred penetrations were made at 1-meter intervals along 50 meters of tape line at two separate locations inside the trapping grid.

Results

Only two species of small mammals were captured during nine trap sessions, amounting to 3890 trap nights (Table 1). These were the Great Basin pocket mouse, *Perognathus parvus,* and the deer mouse, *Peromyscus maniculatus.*

Pocket Mice. Peak catches of pocket mice occurred in September and April with 35 and 30 animals, respectively, and a crude estimate of 4.50 to 5.25 individuals per acre can be made. This figure was far below the 53 animals per acre estimate of O'Farrell

TABLE 1. Number of small mammals trapped at different seasons of the year.

	1973						1974					
	Jul	Aug	Sep	Oct*	Nov	Dec*	Jan	Feb*	Mar	Apr	May	Jun
Perognathus p.												
Male	8	12	20		0		0		12	20	9	5
Female	6	10	15		2		0		1	10	15	4
Total	14	22	35		2		0		13	30	24	9
Peromyscus m.												
Male	0	0	0		1		5		4	6	3	0
Female	0	0	0		1		1		1	1	1	0
Total	0	0	0		2		6		5	7	4	0

* Traps not opened.

et al. (1974) for a plot on the Arid Lands Ecology Project located west of the study area. Pocket mice were not active aboveground in winter. A reduced catch of pocket mice in summer probably reflects the onset of aestivational behavior. The March catch was comprised almost entirely of males, indicating early emergence of males from hibernation; however, females dominated the catch in May. The greatest overall catch of males is partly a reflection of their wider movements. More males were trapped than females in seven out of nine trap sessions.

Of the 35 marked animals active on the trap grid in September, 30 were trapped the following April and comprised the entire April catch, i.e., no new animals were trapped. This finding indicates that there was little migration in the spring. Males demonstrated somewhat larger areas of activity than females, especially in spring (Fig. 3). This situation was also reported by Maza *et al.* (1973) and O'Farrell *et al.* (1974) and is probably caused by males ranging over large areas during the breeding season in search of females, or simply because the males, being larger, require a larger range and greater food requirements.

The average body weight of male pocket mice was significantly greater than that of females. Males averaged 15.6±0.6 (standard error) as compared with 14.2±0.5 grams for females. Schreiber (1973) reports body weights from 380 trap-killed pocket mice. Males averaged 17.7 grams as compared with 14.4 for non-gravid females. Gravid females averaged 16.7 grams. Body weights of the pocket mouse population changed seasonally (Fig. 4). Mice were heaviest in May and lightest in August, probably due to the inflx of sub-adults into the population.

The low population of pocket mice in knob and kettle topography is attributed to stony soil and the lack of burrow sites rather than to differences in kinds or quality of foods provided by herbaceous plant species. The stoniness of the soil is illustrated in Figure 5. Maximum soil depth over rocks was 7 dm with an average depth of 3.4±1.9 dm.

During the same time period as this study, an area with an average penetrable soil depth of 7.4±2.0 dm was trapped and was found to support over three times as many small mammals.

Deer Mice. Deer mice were active aboveground in winter and disappeared from the trap catches in summer. The maximum number of deer mice was trapped in April

when only seven mice were caught (Table 1). Deer mice on the average were heavier than pocket mice. Males averaged 19.9±0.9 grams and females 18.2±2.2 grams.

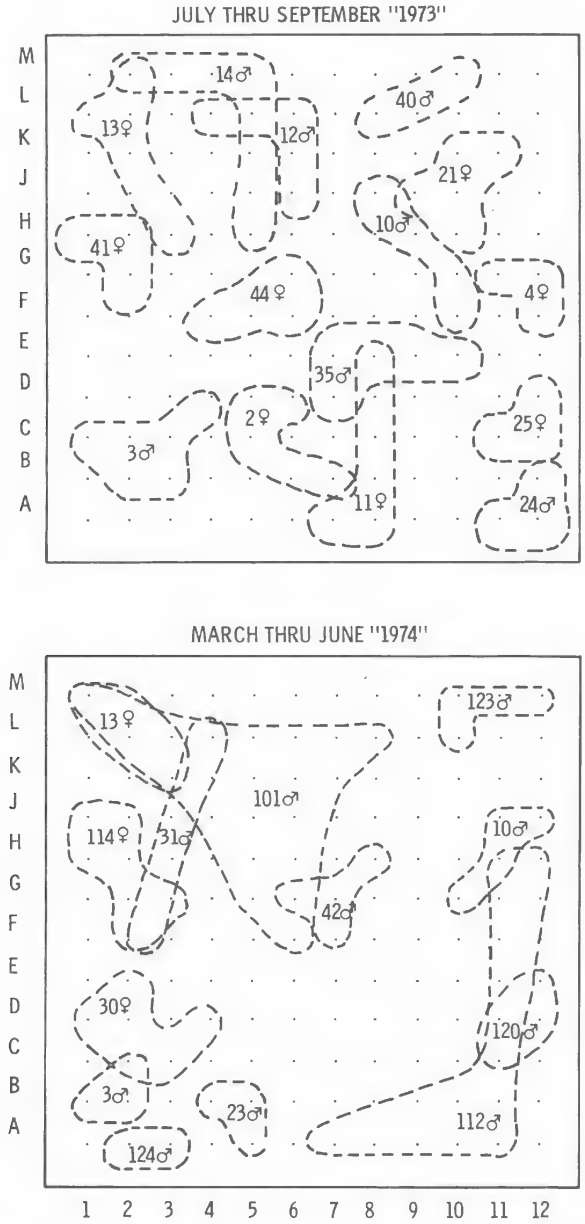


Figure 3. Areas of activity of selected pocket mice plotted in the 12 x 12 trap grid, July through September 1973, upper grid, and March through June 1974, lower grid.

The low population of deer mice is not unexpected because deer mice are characteristically more widely dispersed and occur in much lower numbers than pocket mice.

Discussion

Few mammalian populations are as amenable to trap-mark-recapture studies as pocket mice. For this reason, pocket mice populations are useful for ecological monitoring purposes. Pocket mice are ubiquitous in the shrub-steppe region of south-central Washington. Construction impacts that usurp acreage historically used by mouse

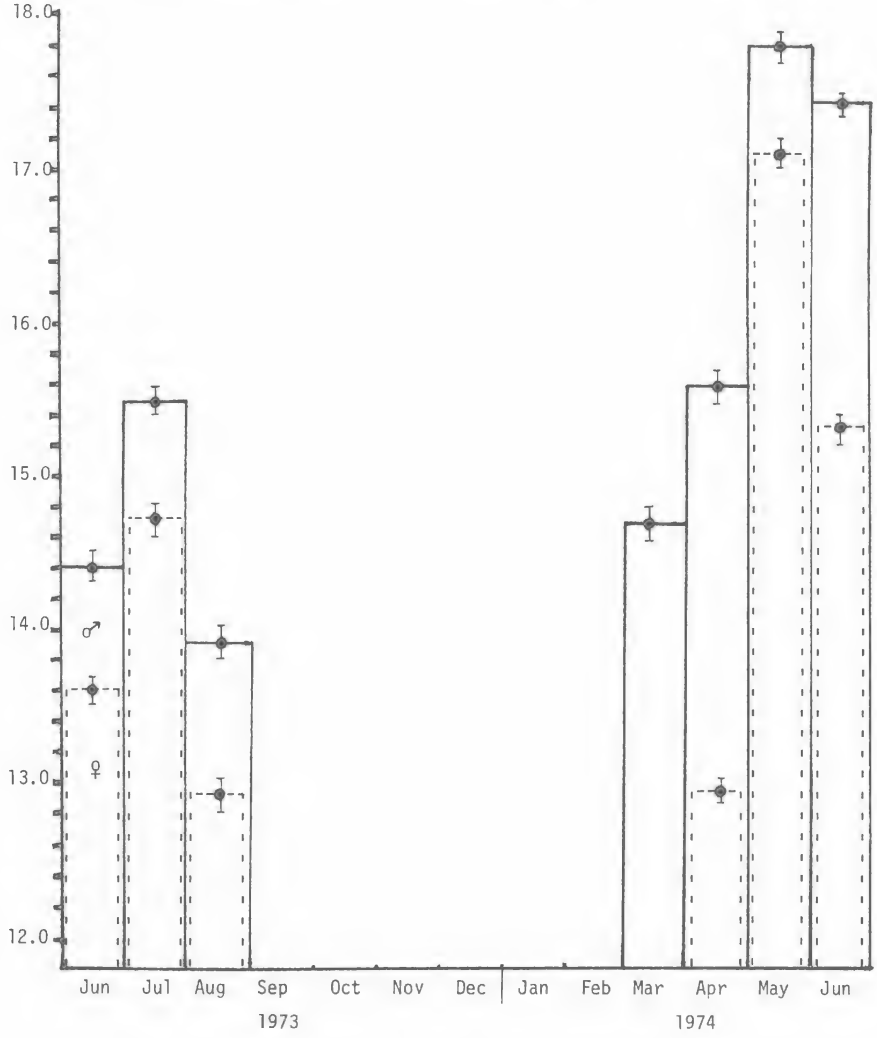


Figure 4. Average weights of pocket mice ± standard error. Females are represented by dotted lines, males by solid lines.

populations can be evaluated in terms of acreage removed from biological production. Because pocket mice are abundant and easily trapped, they can provide biological material that is suitable for radiochemical analyses although individual animals provide little biomass. Radionuclide burdens of pocket mice could be indicative of the biological availability of radionuclides in confined areas because pocket mice have small activity areas (Fig. 3). Because mice are not normally eaten by people, they are not monitored for radiological health purposes; they most certainly contain small amounts of radionuclides from fallout material. Small mammals do provide a food base for birds of prey and mammalian predators. Pocket mice can be repeatedly captured, and this circumstance permits estimations of their longevity under field environments as well as opportunities to record changes in body weight and to observe their general health and condition.

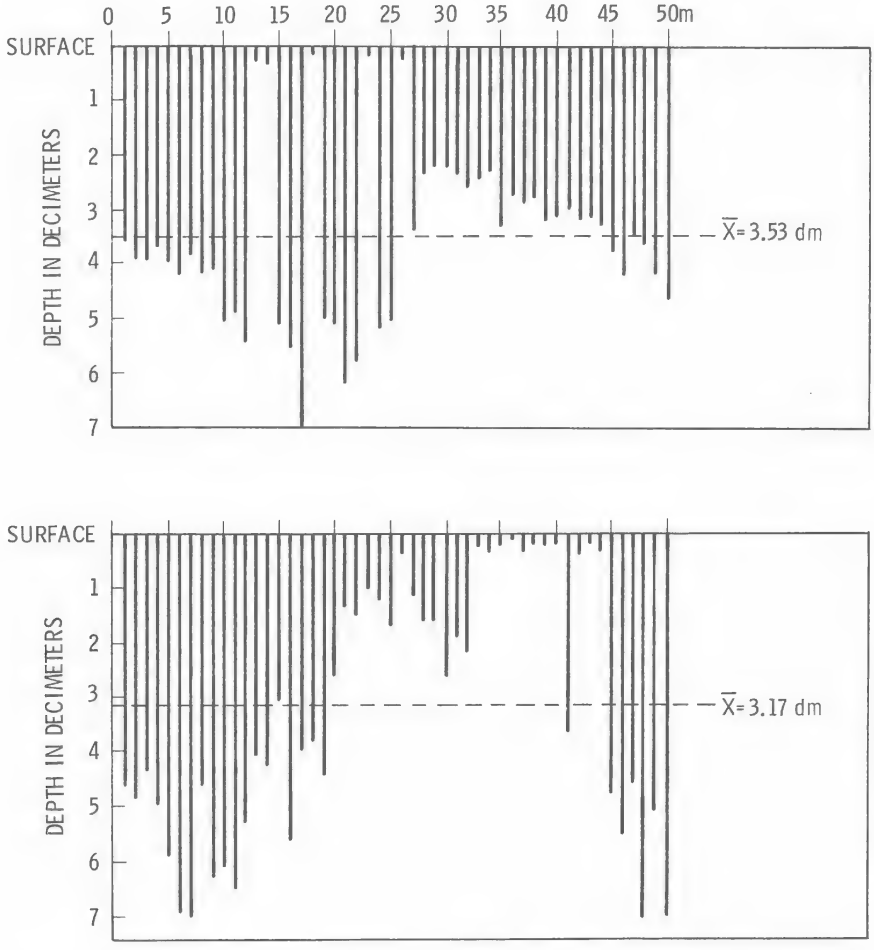


Figure 5. Soil-depth measurements determined by metal-rod penetrations.

The population of pocket mice in knob and kettle terrain has experienced the airborne effluents from the operating N-reactor since 1963. Although detailed terrestrial ecology baseline studies were not made prior to the start-up of the reactor, we believe that the small increments of added radioactivity have not had any measurable ecological impact on the nearby mouse population. Thermoluminescent dosimeters (TLD's) have been used to measure radiation doses at the 100-N reactor site (Bramson *et al.,* 1973). In 1972 dosimeter measurements averaged 0.29 mR/day as compared with an off-site background of 0.22 mR/day. O'Farrell *et al.* (1972) reported on the effect of large doses of acute ionizing radiation on a free-ranging pocket mouse population. The $LD_{50/30} \pm 5.0$ value derived was 834±32 rad. (834,000 mR).

Many of the individuals which received sublethal doses were captured on the study area up to three years postirradiation. Of the survivors, females did not recover from radiation-induced sterility although 20 of 24 irradiated males displayed scrotal testes one-two years later. When compared with data obtained from a laboratory-confined population, there were no differences in survival between these and free-ranging pocket mice.

The acute radiation doses delivered to pocket mice for observable differences in performance and survival were far greater than the near-background doses measured near the N-reactor.

Hanson (1960) measured the accumulation of radioisotopes by terrestrial animals on the Hanford Reservation and concluded that isotopic body burdens were mostly derived from worldwide fallout rather than effluents from nuclear operations. Hence, the low population on the knob and kettle area is attributed to the stoniness of the soil substrate rather than to environmental stresses imposed by the construction and operation of the nuclear power station.

Literature Cited

Bramson, P. E., J. P. Corley, and W. L. Nees. 1973. Environmental status of the Hanford Reservation for CY-1972. BNWL-B-278.

Hanson, W. C. 1960. Accumulation of radioisotopes from fallout by terrestrial animals at Hanford, Washington. Northwest Sci. 34: 89-98.

Kritzman, E. B. 1974. Ecological relationships of *Peromyscus maniculatus* and *Perognathus parvus* in eastern Washington. J. Mammal. 55: 172-188.

Maza, B. G., N. R. French, and A. P. Aschwanden. 1973. Home range dynamics in a population of heteromyid rodents. J Mammal. 54: 405-425.

O'Farrell, T. P., J. D. Hedlund, R. J. Olson, and R. O. Gilbert. 1972. Effects of ionizing radiation on survival, longevity, and reproduction in free-ranging pocket mice, *Perognathus parvus.* Radiat. Res. 49: 611-623.

O'Farrell, T. P., R. J. Olson, R. O. Gilbert, and J. D. Hedlund. 1974. A population of Great Basin pocket mice, *Perognathus parvus,* in the shrub-steppe of south-central Washington. Ecological Monographs (in press).

Rickard, W. H. 1974. Vegetation of knob and kettle topography in south-central Washington (manuscript).

Schreiber, R. K. 1973. Bioenergetics of rodents in the northern Great Basin desert. Ph.D. Dissertation, U. of Idaho, Moscow. 133 p.

Received May 29, 1975.
Accepted for publication June 20, 1975.

Ronald A. Nussbaum

Museum of Zoology and
Department of Zoology
University of Michigan
Ann Arbor, Michigan 48104

and

Chris Maser

Puget Sound Museum of Natural History
University of Puget Sound
Tacoma, Washington 98416

Food Habits of the Bobcat, Lynx rufus, in the Coast and Cascade Ranges of Western Oregon in Relation to Present Management Policies

Abstract

The food habits of bobcats were studied in the Coast and Cascade Ranges of western Oregon. Food was determined by analysis of the contents of randomly collected scats. Rabbits occurred in 52.5% of the scats (n=143) from the Coast Range and in 70.6% of the scats (n=34) from the Cascade Range. Weight-frequency relationships of prey indicate that rabbits are the most important food of bobcats in these regions. Rodents were present in 70.0% and 82.3% and insectivores in 2.2% and 5.8% of the scats from the Coast and Cascade Ranges, respectively. Deer, probably carrion, were present in 2.1% and 2.9% of the scats. Remains of domestic sheep were found in 0.7% of the scats from the Coast Range, but were not observed in scats from the Cascade Range. Bird remains occurred infrequently in both samples. In light of these results, and because of the rapidly rising price of bobcat pelts, we suggest that the current management practices for bobcats in Oregon badly need revision. Bobcats should be removed from the status of "predatory animal" and be given the status of "fur-bearer" with the provision that control measures may be carried out on a local, problem-area basis if proved necessary.

Introduction

The bobcat, *Lynx rufus,* a medium-sized predator, occupies diverse habitats throughout most of the United States and Mexico. Two subspecies occur in Oregon: *fasciatus,* found largely in coniferous forests west of the crest of the Cascade Range, and *pallescens,* a subspecies of open sagebrush plains and rocky canyons confined east of the crest of the Cascade Range (Hall and Kelson, 1959).

According to Mace (1974) "Oregon law currently classifies the bobcat as a predator which may be taken by any means and any time of the year," and he estimated that 4500 bobcat pelts were sold by Oregon fur trappers during the 1973/74 trapping season for an estimated $250,000. Bobcats are currently being killed by licensed and nonlicensed fur trappers, federal trappers, sport hunters, hound hunters, and landowners. As late as 1972, 10 Oregon counties (mostly western counties) paid bounties on 935 bobcats (Robert U. Mace, pers. comm.). In Oregon bobcats may be killed legally even during the breeding season when their pelts are still commercially valuable. Since the commercial value of pelts has soared (Mace, 1974), there is need to reevaluate the bobcats' economic status, population status, and future as the world's only spotted cat allowed unlimited harvesting (IUCN, 1972).

Bobcats are secretive and not easily observed in the field, and population densities or trends within a given area are difficult to estimate. Only through the study of its food habits can we begin to evaluate the bobcats' role in man's economy. Gashwiler *et al.* (1960) reviewed the literature on bobcat food habits, revealing a dearth of such information for Oregon. The purpose of this paper, therefore, is twofold: (1) to present new data on the food habits of bobcats in western Oregon, and (2) to show how these data relate to current management policies.

Methods

During the years 1970-72 we routinely collected scats of carnivores in western Oregon while engaged in various field activities. In the Coast Range, bobcat droppings were collected at many localities, nearly spanning the length of the Oregon Coast. In the Cascade Range, however, most scats were collected within the H. J. Andrews Experimental Forest, Lane and Linn counties.

Prey were identified from bones, teeth, hair, claws, feathers, and other recognizable remains. Prey were determined to species only when diagnostic parts were available, or when only one species of a genus occurred in the region where the scat was collected. The number of individuals of each prey within a scat was estimated, but this is a minimum estimate since some parts may represent more individuals than we could definitely count. For example, two skulls were scored as two individuals, but three molars were scored as only one prey even though three prey could conceivably be involved. Average adult weights of the prey were taken mostly from our own records; a few were obtained from the literature. Because of the method of collecting we are unable to report seasonal differences in food habits.

Predator-Prey Relationships

Mammals. (1) Lagomorphs: Cottontail rabbits, *Sylvilagus bachmani,* are most abundant along the southern Oregon Coast Range from approximately Gardiner, Douglas Co., southward. Between Gardiner and Florence, Lane Co., brush rabbits and snowshoe hares, *Lepus americanus,* occur together, whereas north of Florence the snowshoe hare is the dominant lagomorph. In the Coast Range, brush rabbits and snowshoe hares occurred in 52.5% of the scats; however, the snowshoe hare, the only lagomorph of the family Leporidae in the Cascade Range, occurred in 79.6% of the scats from that area. It it clear from consideration of weight-frequency relationships of prey (Tables 1 and 2) that lagomorphs are the most important food of bobcats in the Coast and Cascade Ranges. Both cottontail rabbits and snowshoe hares are considered to be detrimental to commercially important timber; they are a "major concern in reforestation" (Canutt, 1969).

(2) Rodents: Rodents occurred in 70.0 and 82.3% of the scats from the Coast and Cascade Ranges, respectively. The deer mouse, *Peromyscus maniculatus,* Oregon vole, *Microtus oregoni,* Townsend vole, *Microtus townsendi,* dusky-footed woodrat, *Neotoma fuscipes,* mountain beaver, *Aplodontia rufa,* Townsend chipmunk, *Eutamias townsendi,* and California ground squirrel, *Spermophilus beecheyi,* occurred in 62.3% of the scats in the Coast Range. In the Cascade Range, the Oregon vole, Mazama pocket gopher, *Thomomys mazama,* Townsend chipmunk, deer mouse, bushy-tailed woodrat, *Neotoma cinerea,* mountain beaver, and California ground squirrel occurred in 47.0% of the

TABLE 1. Food of the bobcat in the Coast Range of Oregon as determined by scat analysis. Number of scats = 143.

Prey	Average adult wt. (g) of prey	No. prey items	Percent of all prey	No. scats in which prey occurred	Percent occurrence
Sylvilagus bachmani	741	65	28.6	63	44.1
Peromyscus maniculatus	24	21	9.3	18	12.6
Microtus oregoni	22	19	8.4	10	7.0
Microtus townsendi	54	18	7.9	12	8.4
Neotoma fuscipes	339	16	7.0	16	11.2
Lepus americanus	1097	12	5.3	12	8.4
Aplodontia rufa	985	12	5.3	12	8.4
Large birds	1000*	12	5.3	12	8.4
Eutamias townsendi	90	10	4.4	10	7.0
Zapus trinotatus	24	9	4.0	8	5.6
Tamiasciurus douglasi	219	7	3.1	7	4.9
Small passerine birds	20*	7	3.1	7	4.9
Spermophilus beecheyi	528	4	1.8	4	2.8
Sorex sp.	4*	3	1.3	3	2.1
Odocoileus hemionus	—	3	1.3	3	2.1
Sorex vagrans	5	2	.9	2	1.4
Beetles	—	2	.9	1	.7
Microtus sp.	25*	2	.9	2	1.4
ruffed grouse	619	1	.4	1	.7
domestic sheep	—	1	.4	1	.7
Arborimus sp.	24	1	.4	1	.7
vegetation	—	—	—	13	9.1
Total		227			

*Crude estimate.

TABLE 2. Food of the bobcat in the Cascade Range of Oregon as determined by scat analysis. Number of scats = 34.

Prey	Average adult wt. (g) of prey	No. prey items	Percent of all prey	No. scats in which prey occurred	Percent occurrence
Lepus americanus	1097	24	39.3	24	70.6
Glaucomys sabrinus	167	6	9.8	4	11.8
Tamiasciurus douglasi	219	4	6.6	4	11.8
Microtus oregoni	22	4	6.6	4	11.8
Thomomys mazama	96	3	4.9	3	8.8
Eutamias townsendi	90	3	4.9	3	8.8
Microtus sp.	25*	3	4.9	2	5.9
Peromyscus maniculatus	24	2	3.3	2	5.9
Neotoma cinerea	346	2	3.3	2	5.9
Aplodontia rufa	985	1	1.6	1	2.9
Spermophilus beecheyi	528	1	1.6	1	2.9
Clethrionomys californicus	24	1	1.6	1	2.9
Neurotrichus gibbsi	10	1	1.6	1	2.9
Zapus trinotatus	24	1	1.6	1	2.9
Sorex sp.	4*	1	1.6	1	2.9
Odocoileus hemionus	—	1	1.6	1	2.9
Gerrhonotus coeruleus	20	1	1.6	1	2.9
grouse	830*	1	1.6	1	2.9
small passerine birds	20*	1	1.6	1	2.9
vegetation	—	—	—	1	2.9
Total		61			

* Crude estimate.

scats. All of these rodents are considered to be detrimental to commercial timber (Canutt, 1969), and some to crops. Continuous and costly control measures are being sought and/or implemented, e.g., a recent campaign has been launched to study and control pocket gopher damage to commercial timber (Barnes, 1973). Rodents, such as the Pacific jumping mouse, *Zapus trinotatus,* chickaree, *Tamiasicurus douglasi,* northern flying squirrel, *Glaucomys sabrinus,* and voles, *Arborimus,* which are of little or no detrimental economic importance occurred in 11.2 and 29.4% of the scats from the Coast and Cascade Ranges, respectively.

(3) Insectivores: Shrews, *Sorex* sp., and shrew-moles, *Neurotrichus gibbsi,* occurred in 2.2 and 5.8% of the scats from the Coast and Cascade Ranges, respectively. The shrews are considered to be detrimental to commercial timber by eating the seeds (see Kangur, 1954; Moore, 1942), but shrew-moles may be wholly beneficial by destroying many invertebrates.

(4) Artiodactyls: Deer, *Odocoileus hemionus,* occurred in 2.1 and 2.9% of the scats from the Coast and Cascade Ranges. Although the deer remains were those of fawns, as indicated by size of hoofs, and might have been killed by bobcats, they may have been carrion. Domestic sheep, *Ovis* sp., occurred in 0.7% of the scats from the Coast Range, and did not occur in scats from the Cascade Range.

Birds. (1) Passerine birds: Most of the small passerine birds were sparrows which nest close to or on the ground.

(2) Marine birds: During the winter of 1971 there was a widespread die-off of marine birds along the Oregon coast, primarily murres, *Uria* sp. We observed many of these sick murres and found that they were unable to fly, thus they would have been easily caught by bobcats. The 8.4% occurrence of large birds in the scats from the Coast Range was largely murres, and possibly individuals suffering from disease.

Biological and Commercial Value vs. Legal Statute

Oregon Revised Statute (ORS) 610.002 currently defines the bobcat as a "predatory animal" (Oregon Wildlife Code, 1973/74 edition). Also included in this category are coyotes, red fox, rabbits, rodents, and birds which may be destructive to crops or other valuable resources. ORS 610.005 relegates authority for the destruction, eradication, or control of these predatory animals to the State Department of Agriculture. ORS 610.105 implies that it is the "duty" of every landowner to poison, trap, or otherwise eliminate these "noxious" predatory animals.

Prior to 1961 Oregon maintained a state bounty on bobcats, and since then 10 counties have continued to pay bounties ranging from two to four dollars per bobcat. Even though the state bounty was banned, the Oregon State Wildlife Commission is compelled by ORS 610.020 to set aside 3% of the annual fees from the sale of licenses, fines, and gifts for the control of predatory animals, not to exceed $40,000/annum.

During the four trapping seasons from 1969 70 through 1972/73, 15,976 bobcats were taken in Oregon, exclusive of those killed by hunters and landowners (Mace, pers. comm.). The average price per bobcat pelt climbed from $2.76/pelt in 1957/58 to $55.26/pelt in 1973/74. The average price per pelt from central and eastern Oregon was $78.61 in 1973/74. Annual increments in the price of pelts have been largest since 1970/71 when the average value for all Oregon bobcats was $13.66/pelt

(Mace, pers. comm.). If the price of pelts continues to rise at these rates, trapping and hunting pressure on bobcats undoubtedly will increase enormously.

The results of food-habit studies (V. Bailey, 1936; T. N. Bailey, 1972; Gashwiler *et al.,* 1960; present study) indicate a logical inconsistency in ORS 610.002 which defines bobcats, rabbits, and rodents as predators destructive to agricultural crops and products. Aside from the fact that rabbits and rodents are not predators in the biological sense, to destroy them all seems self-defeating since rabbits and rodents are the major food of bobcats.

Although some domestic birds and mammals are destroyed by bobcats, this situation must not be construed as a generalized, behavioral trait. Bobcat predation on domestic livestock is mostly incidental. There are areas, however, where bobcat predation is a more chronic problem, such as the brushy, western side of the Oregon Coast Range. Good management practices can allow control of bobcats on an individual and/or chronic-problem-area basis. Bounties, on the other hand, waste the taxpayers' money because they are nonselective with respect to the individual bobcat killed. For example, bobcats killed incidentally or for sport on nonagricultural lands or in counties where no bounty exists, can, nonetheless, be sold in nearby counties which still maintain bounties.

V. Bailey (1936) stated that sheep remains were found in 27 out of 200 bobcat stomachs from eastern Oregon. He also stated that 3 stomachs contained deer meat, and 95 contained ". . . rabbits of the four common species." T. N. Bailey (1972) studied aspects of the bobcats' life history in east-central Idaho and found results similar to ours. He reported that jackrabbits and cottontails made up more than 90% of the diet, with rodents and birds the next most frequently eaten food. Only one of the 300 stomachs which he examined contained the remains of sheep; furthermore, he cited a study which showed that 23 of 26 deer eaten by bobcats were carrion. Although bobcats can and do kill some deer and sheep, we suspect that many of the deer and sheep remains which appear in bobcat stomachs and scats represent carrion. Nevertheless, both deer and sheep are very minor components of the bobcats' diet, to the extent that any cost/benefit analysis would surely favor the bobcat for its role in lagomorph and rodent control.

Conclusions

In light of the results of food-habit studies, and because of the increasing value of bobcat pelts, we strongly urge that the public and responsible officials review the economic status of the bobcat in Oregon and consider its reclassification. A logical first step would be to remove the bobcat from the status of "predatory animals" and to place it in the status of fur-bearer, with provisions that, when shown (or proved) necessary, proper control measures may be carried out.

Acknowledgements

We thank Carol Fieber and Cynthia Tait for helping with the analysis, and Eric Forsman for identifying the birds. Rita Maser, Laurel Keller, Jon Skovlin, and Charles Henny edited the manuscript. Gene Silovsky helped collect scats. The study was supported in part by the National Science Foundation Grant No. GB-20963 to the Coniferous Forest Biome, U.S. Analysis of Ecosystems, International Biological Program;

and in part by the Oregon Coast Ecological Survey, Puget Sound Museum of Natural History, University of Puget Sound. This is contribution No. 185 from the Coniferous Forest Biome.

Literature Cited

Bailey, T. N. 1972. The elusive bobcat. Natural History 81(8): 43-49.
Bailey, V. 1936. The mammals and life zones of Oregon. North American Fauna No. 55. U.S.D.A. Bureau Survey. 416 pp.
Barnes, V. G., Jr. 1973. Pocket gophers and reforestation in the Pacific Northwest: a problem analysis. [U.S.] Fish and Wildl. Service, Special Sci. Report: Wildl. No. 155. 18 pp.
Canutt, P. R. 1969. Relative damage by small mammals to reforestation in Washington and Oregon, *in* H. C. Black, ed., pages 55-59, Wildlife and reforestation in the Pacific Northwest. Oregon State University, Corvallis.
Gashwiler, J. S., W. L. Robinette, and O. W. Morris. 1960. Foods of bobcats in Utah and eastern Nevada. J. Wildl. Mgmt. 24: 226-229.
Hall, E. R. and K. R. Nelson. 1959. *The mammals of North America.* Vol. 2. Ronald Press Co., N. Y.
IUCN. 1972. Red Data Book, Vol. I: Mammalia, compiled by H. A. Goodwin and C. W. Holloway. Morges, Switzerland.
Kangur, R. 1954. Shrews as tree seed eaters in the Douglas fir region. Oregon State Board of Forestry, Research Note 17. 23 pp.
Mace, R. U. 1974. The bobcat is in trouble! Oregon Wildlife 29: 3-4.
Moore, A. W. 1942. Shrews as a check on Douglas fir regeneration. J. Mammalogy 23: 37-41.

Received May 2, 1975.
Accepted for publication June 2, 1975.

Theodore H. Blahm
and
George R. Snyder

Northwest Fisheries Center
2725 Montlake Boulevard East
Seattle, Washington 98112

Effect of Increased Water Temperatures on Survival of Adult Threespine Stickleback and Juvenile Yellow Perch in the Columbia River

Abstract

Flow-through bioassay tests on the effects of temperature increases on yellow perch (*Perca flavescens*) and threespine stickleback (*Gasterosteus aculeatus*) were conducted on the lower Columbia River near Prescott, Oregon. The on-site tests of two weeks' duration were performed on (1) control samples of fish at a water temperature of 19° C and (2) on test samples of fish at water temperatures of 20°-26° C—in 1-degree increments—and at 29°, 32° and 38° C. Samples of threespine stickleback reached 50% mortality at 25° C in 1,725 minutes, and samples of yellow perch reached 50% mortality in 143 minutes.

Introduction

Water-temperature criteria for species of fish associated with Pacific salmon (*Oncorhynchus* spp.) and steelhead trout (*Salmo gairdneri*) in the lower reaches of the Columbia River are noteworthy because of a probable increase in water temperature resulting from man's activities. Irrigation, hydroelectric developments, and the discharge of hot water from nuclear power plants could cause displacement of some salmon and steelhead trout by "warm water" species of less value to fishermen than the salmon and trout. We studied survival of juvenile yellow perch (*Perca flavescens*) and adult threespine stickleback (*Gasterosteus aculeatus*) at several temperatures to obtain information on their tolerance above ambient river temperatures which ranged from 17° to 21° C. Yellow perch and threespine stickleback were selected for our study because they are abundant in some areas of the lower Columbia (McConnell and Snyder, 1970) and could displace some salmon and trout if environmental conditions were altered in their favor. In the literature there is little reference to the preferred temperature range of the threespine stickleback. Juvenile yellow perch tested in Ontario, Canada, had a preferred temperature of 24.2° C (Ferguson, 1958); juvenile chinook salmon (*O. tshawytscha,* which are very abundant at certain times in the lower Columbia River), tested in British Columbia, Canada, had a preferred temperature of 12° to 14° C (Brett, 1952).

Experimental Procedures

The fish were captured with a beach seine and transported in a holding tank by boat to the NMFS (National Marine Fisheries Service) experimental water temperature laboratory near Prescott, Oregon (Snyder, Blahm, and McConnell, 1971). The perch were captured on July 10 and the stickleback on July 25, 1969. Transport of fish to

the laboratory required about 10 min; river water was circulated through the holding tank during transport. At the laboratory the fish were transferred to large holding tanks (2500 liters) and held four days prior to testing. The holdings tanks were supplied with Columbia River water which was circulated at a rate of about one interchange per hour (Snyder, Blahm, and McConnell, 1971). The juvenile yellow perch and adult threespine stickleback averaged 49 mm and 37 mm, respectively, in length.

The general methods followed for these tests of thermal tolerance were those outlined by Fry (1947) and used by Brett (1952). The specific test procedure followed in this study is described by Blahm and McConnell (1970, 1971). The thermal tolerance tests were conducted on juvenile yellow perch beginning July 14, 1969, and on the adult threespine stickleback beginning July 29, 1969. The ambient temperature of the Columbia River water (19° C at the beginning of the tests) was used as the control temperature. The fish were placed in 188-liter tanks with preset water temperatures of 19° (control), 20°, 21°, 22°, 23°, 24°, 25°, 26°, 29°, 32°, and 38° C. Separate groups of yellow perch and 10 threespine stickleback were tested at each temperature. The time to mortality was recorded for each fish. The duration of the tests with each species was two weeks.

Tolerance of Fish to Increased Water Temperatures

Juvenile yellow perch reached 50% mortality at 32° C; adult threespine stickleback were less tolerant and reached 50% mortality at 26° C (Table 1). Both species were more resistant to a higher water temperature than juvenile chinook salmon (Fig. 1) tested at the same facility.

Significance of Increased Water Temperature to Fish Populations in the Lower Columbia

The above data suggest that juvenile yellow perch and adult threespine stickleback can withstand water temperatures that cause stress to Pacific salmon and steelhead trout. In addition, the data suggest that yellow perch could be among the species displacing juvenile salmon and trout if water temperature of the Columbia should rise to 20°-25° C. The

TABLE 1. Time to death (in minutes) of adult threespine stickleback and juvenile yellow perch, subjected to elevated water temperatures. The 5%, 50%, and 100% mortality levels are shown for samples of 20 fish each.

Temperature	Threespine stickleback[1] (Time to death by percent)			Yellow perch[2] (Time to death by percent)		
(°C)	5%	50%	100%	5%	50%	100%
			Minutes to death			
19[3]	4,120	—	—	—	—	—
20	4,118	—	—	—	—	—
21	4,116	—	—	—	—	—
22	4,115	—	—	—	—	—
23	4,107	—	—	—	—	—
24	4,110	—	—	18,757	—	—
25	4,105	—	—	—	—	—
26	2,669	8,429	—	—	—	—
29	5	120.5	1,425	5,685	—	—
32	1.5	2.3	14	63.7	143.5	191
38	—	—	—	0.40	0.48	0.62

[1] Average weight of 0.5 g and average length of 37 mm.
[2] Average weight of 1.2 g and average length of 49 mm.
[3] Control and acclimation temperature.

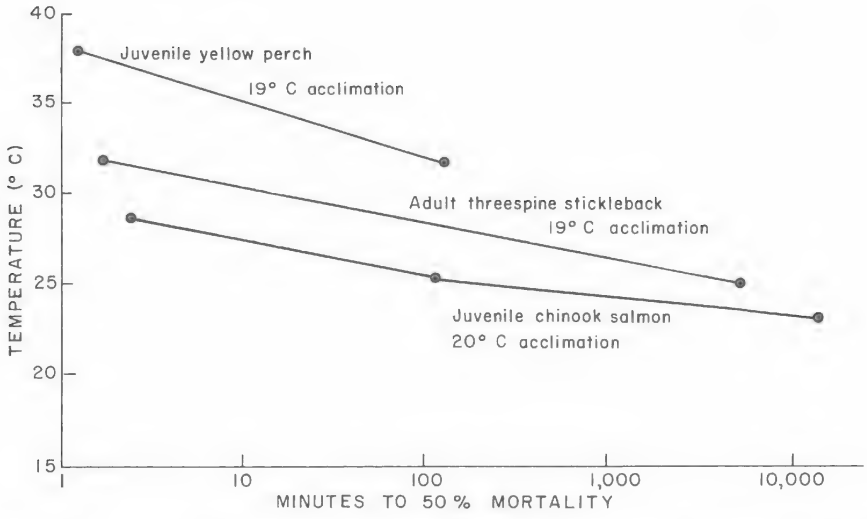


Figure 1. Temperature level and time required to produce 50% mortality in samples of juvenile perch, adult stickleback, and juvenile chinook salmon.

adult threespine stickleback seem to prefer a lower water temperature than do the juvenile yellow perch and would also have an advantage over salmon and trout at temperatures above 20° C. Although not tested in this study, species such as carp (*Cyprinus carpio*), bass (*Micropterus* spp.), and sunfish (*Lepomis* spp.) have been reported to prefer water temperatures above 20° C (Ferguson, 1958). These warm-water fishes are present in the lower Columbia River near Prescott (McConnell and Snyder, 1970) and would also be among the species capable of displacing salmon and trout if environmental conditions were altered in their favor.

Summary

1. Adult threespine stickleback reach 50% mortality at 26° C. 2. Juvenile yellow perch reach 50% mortality at 32° C. 3. Both species are able to withstand temperatures that would produce substantial mortalities in salmonid populations.

Literature Cited

Blahm, T. H., and R. J. McConnell. 1970. Effect of increased water temperatures on the survival of spring and fall juvenile chinook salmon (*Oncorhynchus tshawytscha*) from the lower Columbia River. Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Northwest Fish. Center, Seattle, Wash., 7 p., 2 figs. (Processed.)

Blahm, T. H., and R. J. McConnell. 1971. Mortality of adult eulachon (*Thaleichthys pacificus*) subjected to sudden increases in water temperature. Northw. Sci. 45: 178-182.

Brett, J. R. 1952. Temperature tolerance in young Pacific salmon, genus (*Oncorhynchus*). J. Fish. Res. Board Can. 9: 265-323.

Ferguson, R. G. 1958. The preferred temperature of fish and their mid-summer distribution in temperate lakes and streams. J. Fish. Res. Board Can. 15: 607-624.

Fry, F. E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud., Biol. Ser. 55 (Publ. Ontario Fish. Res. Lab. 68). 62 p.

McConnell, R. J., and G. R. Snyder. 1970. Occurrence of fish in the vicinity of proposed sites of two nuclear electric plants on the lower Columbia River. Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Northwest Fish. Center, Seattle, Wash. 30 p. (Processed.)

Snyder, G. R., T. H. Blahm, and R. J. McConnell. 1971. Floating laboratory for study of aquatic organisms and their environment. U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Circ. 356, 16 p.

Received April 1, 1975.
Accepted for publication June 10, 1975.

Association News

The fall meeting of the Association took place in Cheney, Washington, with 19 officers, trustees and section officers in attendance.

It was determined that the Association business was in order and the Association solvent.

Jack Fletcher has resigned as trustee and will be replaced.

The 1977 meeting is being planned for the Oregon College of Education campus in Monmouth, Oregon.

The following appointments were made by President Gilmour.

Grants Committee—Kiver, Diettert and Horner
AAAS Representative—Gilmour
Citations Committee—Nicol, Deitschman, Broderson
Historical—Kiser, Merriam
Auditing—Ettling
Nominations Committee—Stadling, Shrader, Diettrick, Barrett
1976 Meeting General Chairman—Earl Forsman
1976 Meeting General Program Chairman—Don Horner

Plans for a symposium on Ecology of the Northwest, to be held in conjunction with the March 1976 meeting in Cheney, are firmed up and several speakers have accepted.

For those desiring to give papers at the annual meeting, please note the deadline date of January 9, 1976 to get your abstracts to your section chairman and the program chairman Dr. Don Horner at EWSC, Cheney.

Note:

1. Dues were raised at the spring meeting to $7 if paid before January 1, 1976. Otherwise it is $8.
   Students fees are $3 ($4 if paid after January 1).
2. Constitutional changes to be acted upon at the spring meeting.

Article VIII. Amendments *Present Section*

Amendments to this constitution may be made at any annual meeting by a vote of three-fourths of the members present and voting, providing notice of such amendment has been reported in the official program. Proposed amendments must be submitted in writing to the secretary at least three months prior to the annual meeting or published in *Northwest Science,* the official publication of the Association. Proposed amendments presented to the Association must first be approved by the Trustees.

Article VIII. Amendments *Proposed Section*

Amendments to this constitution may be made at any annual meeting by a vote of three-fourths of the members present and voting, providing notice of such amendment has been reported in the official program and has been published in an issue of *Northwest Science* so as to reach the membership at least thirty days before

that annual meeting. Proposed amendments presented to the Association must first be approved by the Trustees.

Article IX. Dissolution

Upon the disolution of the Northwest Scientific Association, the Board of Trustees shall, after paying or making provision for the payment of all of the liabilities of the Association, dispose of all of the assets of the Association exclusively for the purposes of the Association in such a manner, or to such organization or organizations organized and operated exclusively for educational or scientific purposes as the Board of Trustees shall determine and which shall at the time qualify as an exempt organization or organizations under proper provision of the United States Internal Revenue Law.

Milton Mosher, Secretary

Northwest Science

Volume 49, 1975

Bruce V. Ettling, Editor

Published by Northwest Scientific Association and Washington State University Press

Contents

Number 1 (February)

Geomorphic History of the Lower Blue River-Lookout Creek Area, Western Cascades, Oregon 1
Frederick J. Swanson and Michael E. James

Body Measurements of Western Jumping Mice from Northwestern Wyoming 12
Tim W. Clark

Ecological Notes on Deer Mice in Grand Teton National Park, Wyoming 14
Tim W. Clark

Phenological Patterns of Two Alpine Tundra Plant Populations on Niwot Ridge, Colorado 17
M. Fareed and M. M. Caldwell

Ecology of **Artemisia tridentata** subsp. **tridentata** in the State of Washington 24
R. Daubenmire

Plant Succession on Abandoned Fields, and Fire Influences, in a Steppe Area in Southeastern Washington 36
R. Daubenmire

Number 2 (May)

Biosystematics of **Quercus garryana** in Relation to its Distribution in the State of Washington 49
Ronald J. Taylor and Theodore R. Boss

Association News 57

Growth and Dieback of Redstem **(Ceanothus sanguineus)** in Idaho 58
Thomas A. Leege and William O. Hickey

The Ecology of Deadhorse Cave 65
Stuart E. Nixon

Feeling Habits of **Pleocoma** Larvae in Coniferous Forests of Western Oregon 71
David G. Fellin

The Occurrence and Distribution of Mercury in Marine Organisms in Bellingham Bay 87
L. Fraser Rasmussen and Don C. Williams

A Colorado Episode: Beetle Epidemic, Ghost Forests, More Streamflow 95
Nedavia Bethlahmy

Geophysical Survey in South Central Washington 106
Daniela L. Konicek

Number 3 (August)

Effect of Temperature on Growth and Survival of High- and Low-Emission Isolates of **Phellinus (Poria) weirii** 119
Earl E. Nelson and Harland A. Fay

An Analysis of Structural and Functional Characters along a Steppe-Forest Catena 122
R. Daubenmire

An Oil Spill in an Alpine Habitat 141
Joy Belsky

Vegetation of Knob and Kettle Topography in South-Central Washington 147
W. H. Rickard

Tagging Mule Deer Fawns in South-Central Washington, 1969-1974 153
J. D. Hedlund

Characters Useful in Identifying Certain Western Oregon Mammals 158
Chris Maser

Sensitizing Sherman Small-Animal Live Traps To Improve Their Efficiency 160
Bruce A. Evans

Notes on the Vagrant Shrew, **Sorex vagrans,** in the Willamette Valley of Western Oregon 163
E. F. Hooven, R. F. Hoyer, and R. M. Storm

A Middle Tertiary Cetacean from Oregon 174
William N. Orr and John Faulhaber

Number 4 (November)

Litterfall in a Douglas-Fir Forest near the Trojan Nuclear Power Station, Oregon 183
W. H. Rickard

Germination Polymorphism in **Grindelia squarrosa** (Pursch) Dunal 190
W. T. McDonough

Eigenvalue Analysis of an Elastostatic Sector Problem 201
J. W. Weber

Electron Microprobe Analysis as a Test of the Correlation of West Blacktail Ash with Mount St. Helens Pyroclastic Layer T 209
Henry W. Smith, Rose Okazaki, and Charles L. Knowles

Distribution, Reproduction, and Growth of **Crangon nigricauda** and **Crangon franciscorum** in Yaquina Bay, Oregon 216
Earl E. Krygier and Howard F. Horton

Reproduction and Development of the Red-legged Frog, **Rana aurora,** in Northwestern Washington 241
Herbert A. Brown

Mouse Populations on Knob and Kettle Topography in South-Central Washington 253
J. D. Hedlund, D. T. McCullugh, and W. H. Rickard

Food Habits of the Bobcat, **Lynx rufus,** in the Coast and Cascade Ranges of Western Oregon in Relation to Present Management Policies 261
Ronald A. Nussbaum and Chris Maser

Effect of Increased Water Temperature on Survival of Adult Threespine Stickleback and Juvenile Yellow Perch in the Columbia River 267
Theodore H. Blahm and George R. Snyder

Association News 271

Honorary Life Members	Institutional Members
William H. Baker	Boise State University, Boise, Idaho
Ewart M. Baldwin	Central Washington State College, Ellensburg, Washington
Julian D. Barksdale	Clark College, Vancouver, Washington
Irven O. Buss	College of Great Falls, Great Falls, Montana
L. C. Cady	College of Idaho, Caldwell, Idaho
Charles D. Campbell	Eastern Montana College, Billings, Montana
Andrew V. Corry	Eastern Oregon College, LaGrande, Oregon
Julian L. Culbertson	Eastern Washington State College, Cheney, Washington
*Rexford Daubenmire	Evergreen State College, Olympia, Washington
Herman J. Deutsch	Fort Wright College, Spokane, Washington
R. A. Dietlert	Gonzaga University, Spokane, Washington
Bruce V. Ettling	Grays Harbor College, Aberdeen, Washington
James C. Evenden	Green River Community College, Auburn, Washington
William T. Ferrell	Idaho State University, Pocatello, Idaho
C. Clement French	Lewis-Clark State College, Lewiston, Idaho
Stanley P. Gessel	Lewis and Clark College, Portland, Oregon
F. A. Gilfillan	Linfield College, McMinnville, Oregon
N. S. Golding	Malaspina College, Nanaimo, British Columbia
H. P. Hansen	Montana College of Mineral Science & Technology, Butte, Montana
Winslow R. Hatch	Mt. Hood Community College, Gresham, Oregon
Adolph Hecht	Northern Montana College, Havre, Montana
Joseph W. Hungate	Northwest Nazarene College, Nampa, Idaho
Maurice T. James	Oregon College of Education, Monmouth, Oregon
G. Brooks King	Oregon State University, Corvallis, Oregon
Rufus W. Kiser	Oregon Technical Institute, Klamath Falls, Oregon
Lewis and Clark High School Library (in memory of Thomas Large and J. G. McMacken)	Pacific University, Forest Grove, Oregon
Willis B. Merriam	Portland State University, Portland, Oregon
Joseph W. Mills	Seattle Community College, Seattle, Washington
Frank D. Nicol	Seattle University, Seattle, Washington
William A. Rockie	Southern Oregon College, Ashland, Oregon
Francis J. Schadegg	Southwestern Oregon Community College, Coos Bay, Oregon
C. Gardner Shaw	St. Martin's College, Olympia, Washington
Robert F. E. Stier	University of Idaho, Moscow, Idaho
Leona M. Sundquist	University of Montana, Missoula, Montana
Robert F. Tarrant	University of Oregon, Eugene, Oregon
S. C. Vandecaveye	University of Puget South, Tacoma, Washington
Richard B. Walker	University of Washington, Seattle, Washington
*D. J. Wort	Walla Walla College, College Place, Washington
	Washington State University, Pullman, Washington
	Western Washington State College, Bellingham, Washington
	Whitman College, Walla Walla, Washington
	Whitworth College, Spokane, Washington
	Willamette University, Salem, Oregon

*Denotes new additions in 1975.

Sustaining Members	Potlatch Corporation, Lewiston, Idaho Washington Water Power, Spokane, Washington Weyerhauser Company, Centralia, Washington

Change of Address

Send change of address notice to the Treasurer as listed on the inside front cover.

Instructions to Authors

The pages of Northwest Science are open to scientists in the basic, applied, and social sciences wherein original or fundamental research is presented. Manuscripts should be submitted to the Editor, Northwest Science, Washington State University, Pullman, Washington. Prior to submitting manuscripts, authors should request a copy of "Instructions to Authors" from the Editor.

Exchange

Northwest Science is offered in exchange to other colleges, universities, learned societies and libraries. Publications sent in exchange should be addressed to Washington State University Library, Technical Service Division, Pullman, Washington 99163, U.S.A.

Grant A. Harris
Dept. For. & Range Mgt.
Washington State Univ.
Pullman, WA 99163